The Canadian Entomologist

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The Canadian Entomologist

HISTORICAL

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The Canadian Entomologist has been published continuously since 1868. The original Entomological Society of Canada published it until 1871, the Entomological Society of Ontario from 1871 until 1951. A new Entomological Society of Canada was formed in 1951 (see *Can. Ent.* 83: 27-28, 1951), and the two societies published *The Canadian Entomologist* jointly until 1960, when it became the official publication of the Entomological Society of Canada.

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ACKNOWLEDGMENTS

Microctonus aethiops (Nees) auctt. and *Perilitus rutilus* (Nees) (Hymenoptera: Braconidae), European Parasites of *Sitona* Weevils (Coleoptera: Curculionidae)[1]

By CONRAD LOAN[2] AND F. G. HOLDAWAY[3]

Microctonus aethiops (Nees) auctt. (Fig. 1) and *Perilitus rutilus* (Nees) are parasites of adult *Sitona* weevils in Europe. They were released in Canada as control agents of the sweetclover weevil, *Sitona cylindricollis* Fahr. (Fig. 2)[4]. The immature stages and biology of the species were studied as a prerequisite to attempts at biological control. A similar investigation of the braconid *Pygostolus falcatus* (Nees) was completed (Loan and Holdaway, 1961). Jackson (1928) described some aspects of the biology of *P. rutilus*, and additional data are given in the present paper.

Distribution and Hosts

Microctonus aethiops (Nees) auctt. (Fig. 1) and *Perilitus rutilus* (Nees) are Gt. Britain, Berry and Parker (1950) from mass collections of *Sitona* and *Hypera* spp. in France, Kaufman (1923) from a chrysomelid *Phyllotreta vittula* (Redt.) in Germany, Meyer (1934) from *S. hispidula* in Russia, and Newton (1931) from the larva of *Phyllotreta nemorum* (L.) in England. In the present study *M. aethiops* was reared from *S. humeralis* Steph., *S. crinita* Hbst. (=*macularia* Marsh.), and *Hypera postica* Gyll., from France, and from *S. hispidula*, from Sweden.

P. rutilus.—Jackson (1928) summarized the known distribution in continental Europe and the British Isles. The species has not been recorded elsewhere. Jackson reared *P. rutilus* from *S. lineata* (L.) (1928) and *S. hispidula* (1922) in England and Berry and Parker (1950) reared from mass collections of *Sitona* and *Hypera* weevils in France. The species was reared at Belleville from *S. lineata* and *S. hispidula* from Sweden and from *S. humeralis* and *H. postica* from France and also emerged from cocoons obtained from *Sitona* hosts in Italy by Dr. H. L. Parker and staff of the U.S.D.A.

Methods

Methods of study, including separation of larval instars, are similar to those described by Loan and Holdaway (1961) for *Pygostolus falcatus* (Nees). The parasites were reared from live weevils or cocoons and maintained in the Belleville laboratory at 74° F. The cocoons were isolated in one-quarter-dram shell vials to determine the period of pupal development and to permit separation of the

Fig. 1. *Microctonus aethiops* Nees in oviposition posture.

Fig. 2. Male and female *Sitona cylindricollis* Fahr.

males from females at emergence. Weevils collected near Belleville in May and June were exposed to virgin or mated parasites to determine the type of reproduction; others were exposed and then dissected at selected intervals to recover the immature stages and to determine their development. The development of *M. aethiops* was studied in *Hypera meles* (F.), *H. nigrirostris* (F.), and a wide range of *Sitona* species, and that of *P. rutilus* in *S. lineata* and *S. cylindricollis*. The descriptions of the immature stages include minimum and maximum measurements, in microns, of ten specimens followed by the mean in parentheses. The nomenclature of Short (1952) is followed in the descriptions of the larvae.

Parasitized weevils were held in transparent plastic cages (Figs. 3-4). Each of these was made from a round tapered refrigerator container (C) (Tri-State Plastic Moulding Co., Box 337, Henderson, Kentucky) five inches high and 5⅛ inches in diameter at the top. A section (E), one-half inch high, cut from the bottom of the container, was inserted through the top opening and wedged into place about two-thirds of the way down, thus forming a raised floor for the cage. A hole four inches in diameter was cut in the centre of section E and covered with 14-mesh plastic screen. The container lid (A) formed the top of the cage. A four-inch diameter hole cut in its centre for ventilation was covered with 20-mesh plastic screen. An opening was made in each of two sides of the cage for a screw-cap vial (B) to hold foliage in water and a cork (F). The parasite larva drops through the mesh floor on to a tray (D), an additional container lid, where the cocoon is spun in soil or on cloth.

Microctonus aethiops (Nees) auctt.

Identification of M. aethiops

Specimens reared from European weevils and cocoons, and others propagated for four generations, were examined by braconid systematists in North America and Europe. Mr. C. F. W. Muesebeck (Research Branch, U.S.D.A., Washington) and Dr. W. R. M. Mason (Entomology Research Institute, Research Branch, Canada Department of Agriculture, Ottawa) identified the species as *aethiops* (Nees) auctt. This identification was further studied when biological differences between parasites of Swedish and French origin became apparent in the laboratory. Mr. R. D. Eady (British Museum (Natural History), London) concurred with the opinion that the material was *aethiops*, but expressed the possibility that some of it was *secalis* Hal. However, Mr. A. W. Stelfox (formerly of National Museum of Ireland) remounted Haliday's type of *secalis* and found it to be different from the submitted material. [The species is not *labilis* Ruthe, the type of which was examined in London by Dr. Mason.] Dr. Mason concluded after examining various European collections that *aethiops* is the best name for the species pending future revisional work on *Microctonus*.

Biological Strains

The forms of *M. aethiops* from France and Sweden are morphologically similar in the adult and immature stages. They are considered to be biological strains on the basis of differential survival in *S. cylindricollis*. A high proportion of instar I larvae of the French form failed to survive, whereas corresponding mortality of the Swedish form was low or absent. In the laboratory the periods of development of the immature stages were similar. The longevity of the Swedish strain was greater than that of the French strain, but this may not be significant as the Swedish parasites were maintained at a higher relative humidity and were handled less. The seasonal history and host relations may be different:
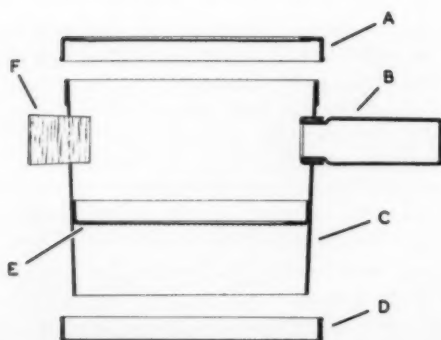
Fig. 3. Parasite emergence cage. Explanation of lettering in text.
Fig. 4. Parasite emergence cage holding parasitized *S. cylindricollis*.

the Swedish form was reared in the autumn from *S. hispidula*, whereas the major emergence of the French form occurred in early summer from *S. humeralis* and *H. postica*.

The Swedish parasites were reared after work on the French form of *M. aethiops* was concluded. In the autumn of 1956, however, a collection of *S. humeralis* obtained from France produced a single female parasite in February, 1957. This female mated with a Swedish male, and four generations were bred in *S. cylindricollis*. A low proportion of larvae were abnormal. They are illustrated in Fig. 13a-e.

Descriptions

Characters to separate the advanced larval instars are not distinct. The transition from one instar to the next is not marked by a distinct change of form.
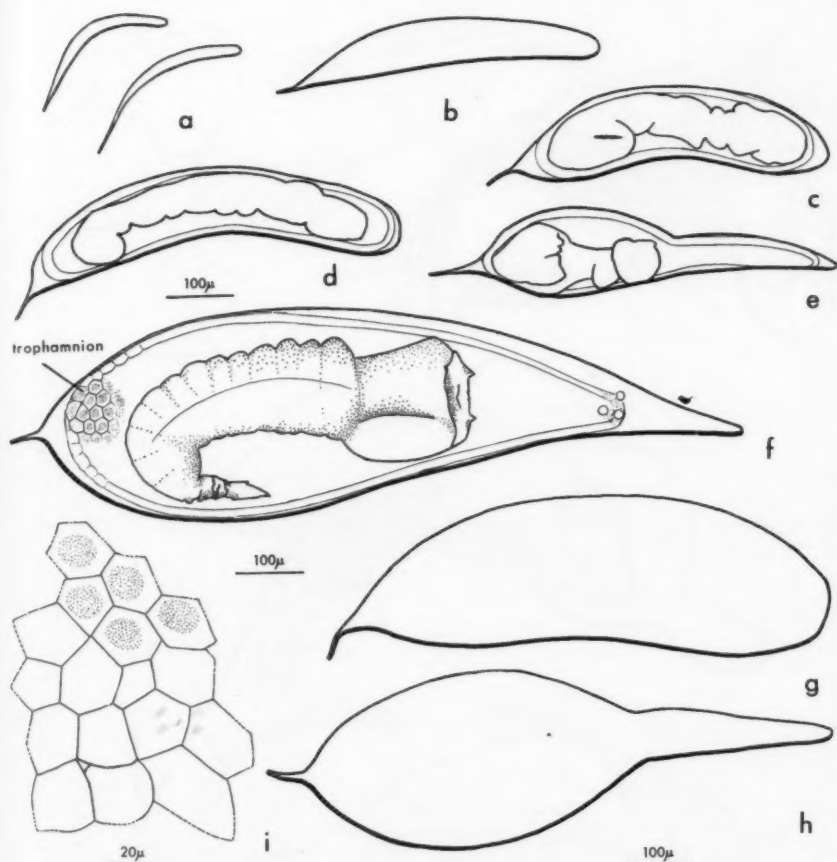
Fig. 5. *Microctonus aethiops*. Development of the egg. a, ovarian egg; b, one day old; c, two days old; d-e, three days old; f-h, four days old; i, trophamnion.

The instar II larva, however, more resembles the mature instar I larva than the grub-like later instars. Mandibles are indistinct and variable in size. They were clearly seen in instars III and IV, and no doubt occur in instar II; those of instar IV are sclerotized and are seen to best advantage on the cast skin. The abdominal cuticle of the instar IV larva is transparent but has a characteristic pattern of brush-like microsetae. This pattern is, however, difficult to see because of the sclerotized cuticle of the developing instar V larva beneath it.

Egg

Length of ovarian egg 185-216 (198) μ from the cephalic end to the tip of the pedicel; width 12-18 (14) μ; length of pedicel about 45 μ. The ovarian egg (Fig. 5a) in lateral view is cylindrical, long and slender, rounded at the cephalic end, and tapered gradually to a narrow pedicel. The growth and shape of the egg after deposition are illustrated in Figs. 5b-h. The form of the mature egg (Figs. 5f-h) is variable. The abdomen of the embryo develops in a curved or semi-curved position; the abdomen and the tail are transparent and the head capsule is faintly melanized.
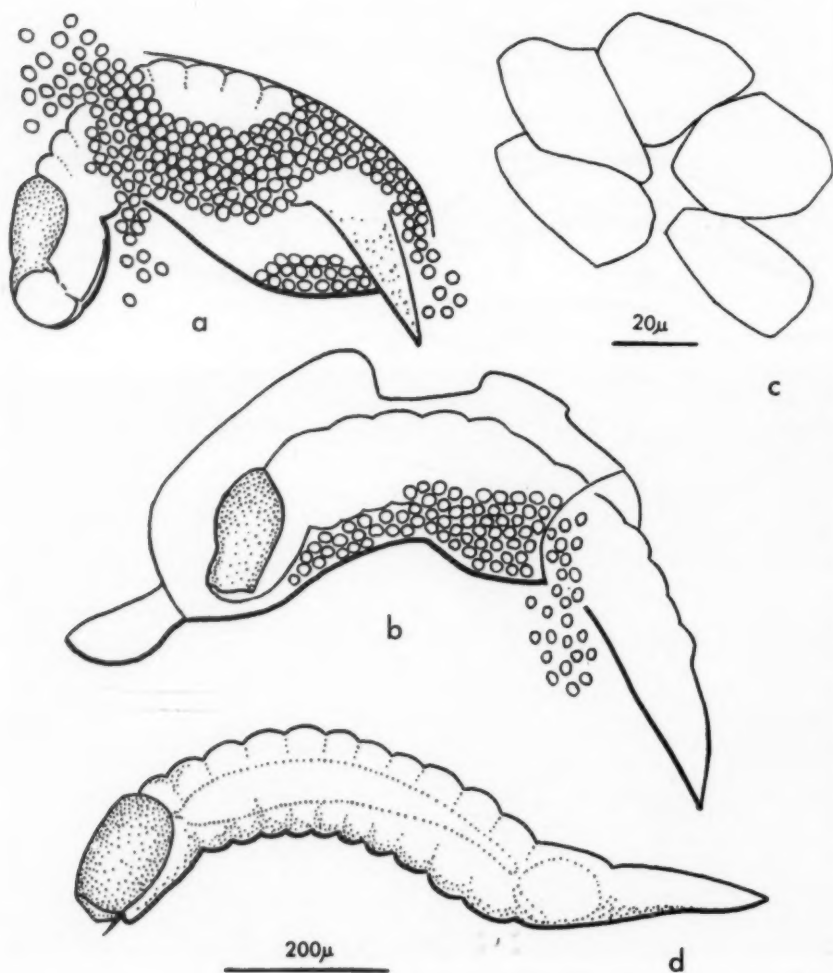
Fig. 6. *Microctonus aethiops*. Hatching of the egg. a-b, embryo struggling out of the chorion; c, dissociating cells of the trophamnion; d, newly-emerged instar I larva.

Instar I Larva

Larva (Fig. 6d) caudate in form, transparent or whitish-yellow in colour. Lengths: newly-hatched larva 1013 μ; diapause larva 1395-1530 (1433) μ; mature larva 1530-2044 (1856) μ; caudal appendage (tail) 203-248 (195) μ; head capsule 180-208 (195) μ; width of head capsule 193-256 (218) μ. Head capsule light stramineous; extended rim of hypopharynx 48-54 (50) μ wide; mandibles falcate, slender, apex 54 μ long and curved into oral opening; antennae lightly sclerotized, cone-shaped, basal diameter 12 μ, height 10 μ, distance between antennae 66-81 (72) μ; one seta 8 μ long mesally of antenna; anterior face with minute roughened and wrinkled patches; microsetae 3 μ long dorsally of oral opening. Tail with microsetae.

400μ

50μ

20μ
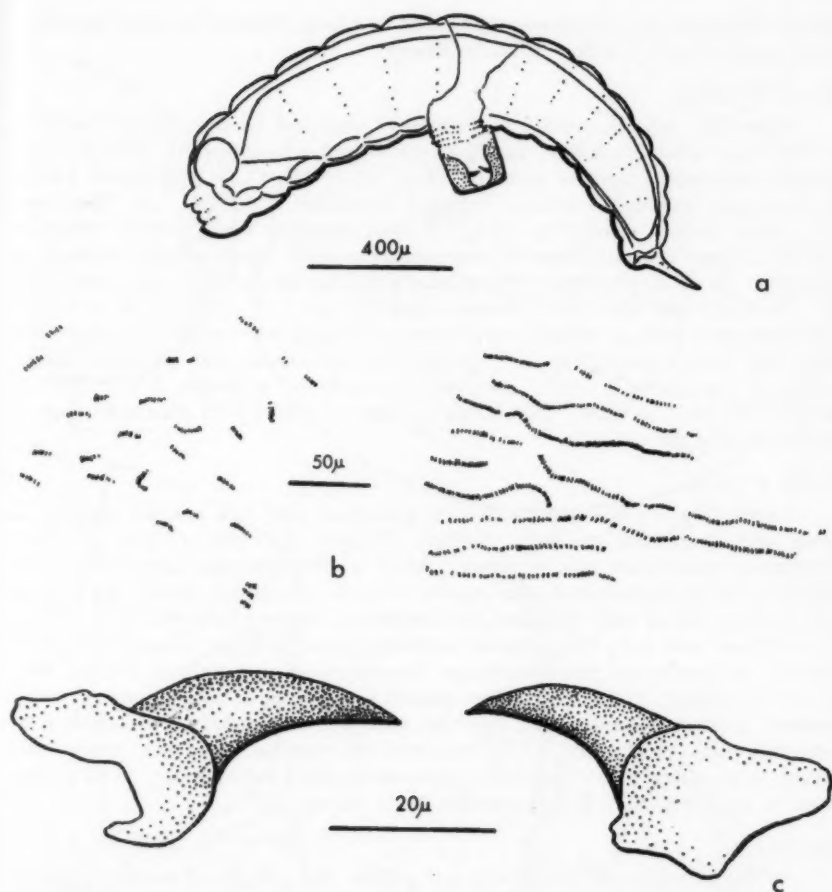
Fig. 7. *Microctonus aethiops*. Larval instar II and IV. a, instar II with head capsule and parts of the cuticle of instar I, and developing cuticle of instar III within; b, brush-like microsetae of cuticle of instar IV; c, cast mandibles of instar IV.

Instar II Larva

Larva (Fig, 7a) similar in general form and colour to the instar I larva. No head capsule and all structures of the head and abdomen unsclerotized. Length 1743 μ (one larva only). The head similar in external outline to that of the instar II larva of *Pygostolus falcatus;* mandibles not seen with certainty. The tail of the abdomen is smooth and enclosed by the cast tail of instar I. Spiracles absent.

Instar III Larva

Similar in form and colour to the previous instar, cuticle unsclerotized, head and prothorax transparent, cast skins of instar I and II adhere to tail of abdomen. Length 1952-2400 (2250) μ. Head in lateral view prognathous and tri-lobed, in anterior view lateral (maxillary) and ventral (labial) lobes border the depressed oral opening; mandibles flat and membranous, very indistinct, situated on either

side of U-shaped rim of hypopharynx, apex 18 μ long, distance between mandibles 64μ; tentorial bar 5 μ wide. Spiracles absent.

Instar IV Larva

Grub-like, whitish-yellow, segmentation obscured by dorsoventral folds of cuticle, microsetae brush-like, mandibles sclerotized. Length 1805-3120 (2272) μ. Head unsclerotized, apex of mandible (Fig. 7c) 12-18 (15) μ long (46-62 (48) μ if basal part included), distance between mandibles 22-84 (47) μ. Characters seen with fuchsin stain (Fig. 8b): flat, oval antenna, labial sclerite complete dorsally, open ventrally; line of sclerotization from labial sclerite to base of mandible (possibly precursor of stipital sclerite and hypostomal spur) extending to sclerotized area mesally of antenna; tentorial bar 5-23 (13) μ wide at centre. Abdomen and parts of thorax with linear pattern of microsetae 2-3 μ high and each line 3-80 μ long (Fig. 7b); spiracles of mesothorax and abdomen closed, spherical (occasionally oval), each in depression of ampullae, I-VII, 20-27 μ wide, VIII, 30-32 μ wide. Film-like cast skins of instars I-III adhere to apex of abdomen (Fig. 8d).

Instar V Larva

Larva (Fig. 9) emerged from host, grub-like, pale dull yellow; sclerites on head and chaetotaxy of body distinct. Length 2250-3846 (2978) μ. Head distinct or withdrawn into prothorax; labial sclerite quadrate, articulating with stipital sclerite; hypostomal spur barely evident; mandibles simple, apex 12-18 (14) μ long (36-52 (40) μ if basal part included), distance between 39-74 (59) μ; labroclypeal setae 6-8 μ long, setae of remaining areas 10-12 μ. Chaetotaxy (three larvae): of prothorax and metathorax, discontinuous dorsoventral line of setae 12-17 in number, 16-52 μ long, interspersed by patches of microsetae; of mesothorax, in three groups, above, opposite, and below spiracle; of abdomen, setae and microsetae of segments I-VIII restricted to ampullae (spiracular group) and raised dorsoventral fold of segment, spiracular group 4-8 in number, 20-50 μ long, setae of segments IX-X, 5-16 in number, 18-54 μ long.

Cocoon

White or yellowish-white, thin and pliable, and consists of an exterior layer of silk and three inner layers of transparent, straw-coloured material laid down by the larva, usually covered by strands of loose silk. If spun in soil it is not easily found because of the particles of soil and surface debris that adhere to it. The skin of the final instar larva is cast near the posterior end and is not readily observed before emergence of the adult.

Adult and Ovaries

Marshall (1887) described the adult. In material reared at Belleville, males are relatively uniform black and females are variable in colour: the thorax may be entirely stramineous, or the episternum and sternum of the mesothorax castaneous and the prescutum and scutum of the mesothorax fuscous. Marshall used the number of segments in the labial palpus as a specific character. This, however, may not be reliable as the number in *M. aethiops* was either two or three and varied between the palpi of individual specimens. The ovaries are paired and each consists of three to six ovarioles (nine females examined) joined distally by connective tissue. There were seven or eight fully developed mature eggs in an ovariole. They occupied the length of the ovariole and no young oöcytes were present.
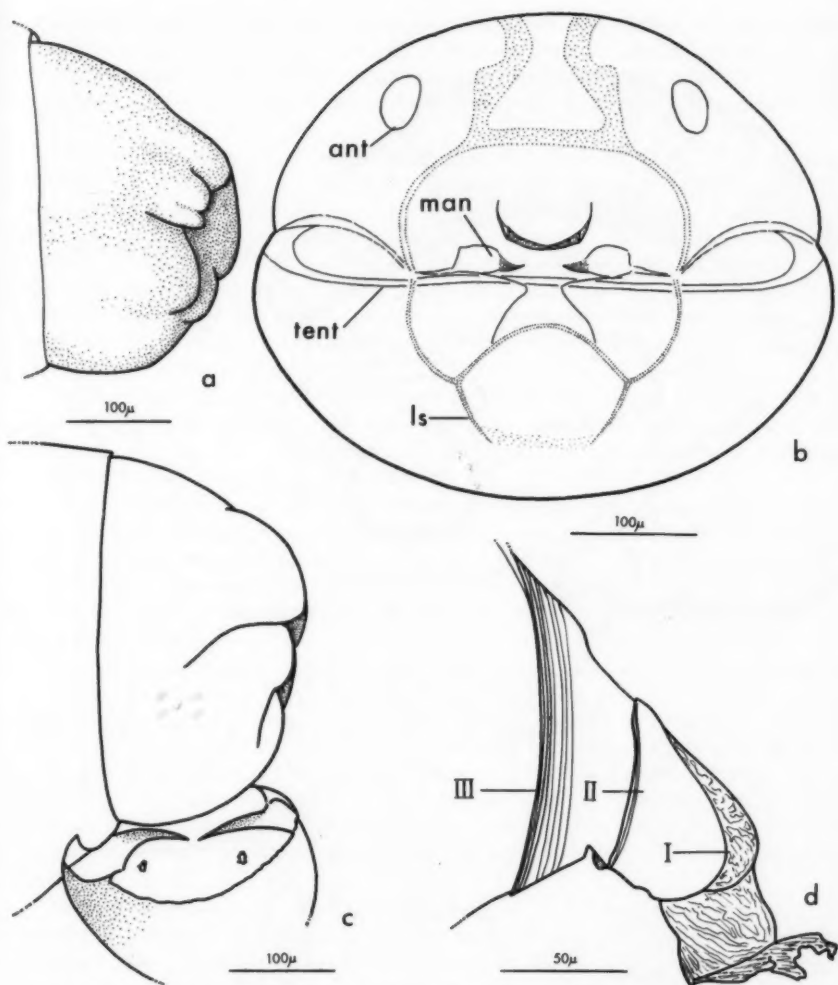
Fig. 8. *Microctonus aethiops*. Larval instar IV. a, lateral view of head of early instar IV larva nine days old; b, anterior view of stained head: ant, antenna; ls, labial sclerite; tent, tentorial bar; c, lateral view of early instar IV larva with attached head capsule of instar I larva; d, complex of cast skins at apex of abdomen: I, instar I; II, instar II; III, instar III.

Biology

Reproduction, Parasitism, and Longevity

Mated females in the laboratory produced progeny of both sexes, and only males resulted from parthenogenetic reproduction. More females than males emerged from cocoons of French origin: from 1952 to 1956 the ratio in 2714 individuals varied from 1.2 to 1.5.

Mating is effected within minutes of emergence and the period of copulation varied from 31-45 seconds. Frequency of copulation is low as males were seen to mate once or twice only. For example, a newly-emerged virgin male mated for
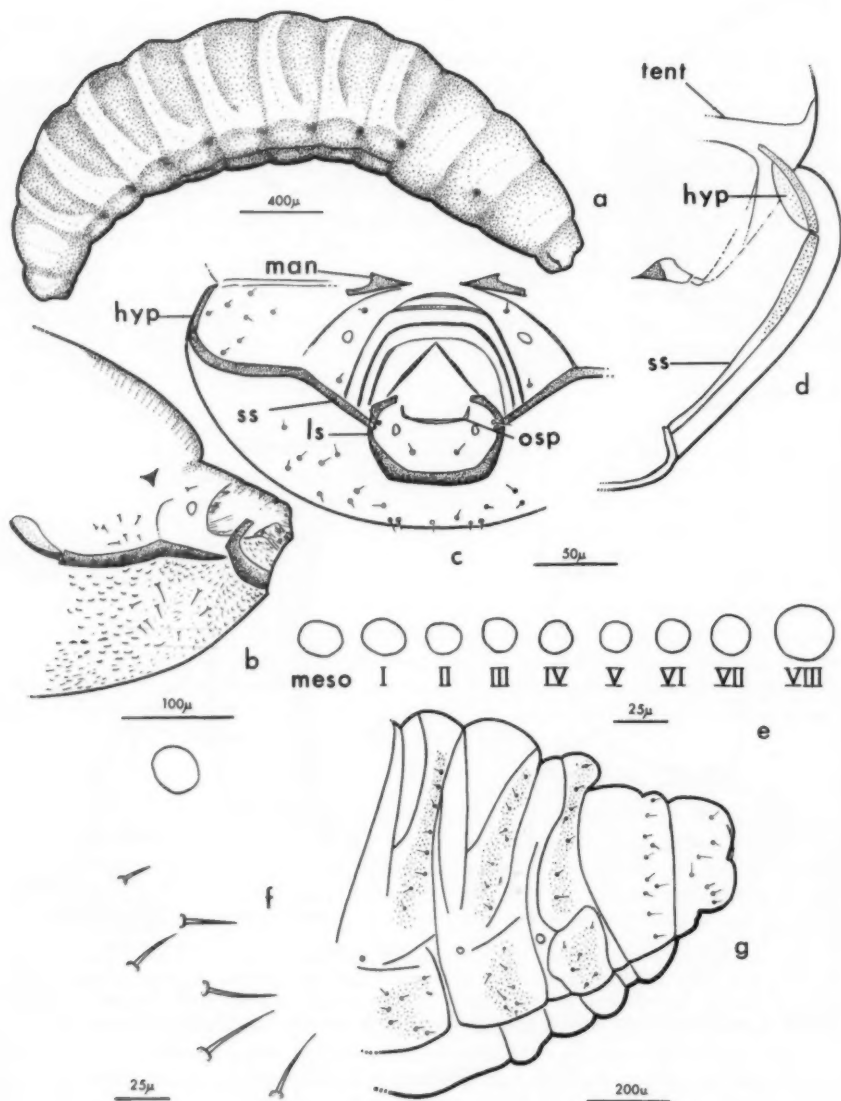
Fig. 9. *Microctonus aethiops*. Larval instar V. a, lateral view of larva; b, lateral view of the head; c, anterior view of the head: hyp, hypostoma; ss, stipital sclerite; d, dorsal view of head; e, thoracic and abdominal spiracles; f, spiracular group of setae; g, abdominal segments VI-X.

38 seconds, then 11 hours later copulated with a second female for 45 seconds. The following day, and again five days later, it showed no interest in a group of virgin females. Numerous observations of a similar kind indicate that the male of *M. aethiops* mates, or attempts to mate, only with virgin or newly-mated females.

Oviposition takes place usually while the adult host is active. It is effected through the membranous area at the apex of the abdomen but may also be attempted, unsuccessfully, in the face or in the thoracic region. A female will take up a position behind a weevil and follow it intently. If the weevil stops, the parasite remains motionless with its antennae extended. If the weevil turns and advances, the parasite may retreat a short distance, move to one side, and then follow it again. When many weevils are present and their paths cross, the parasite may abandon one host for another. She may stalk a weevil for some time without attempting to oviposit.

When ready to oviposit the female extends the ovipositor under and well in front of her head, and makes a quick thrust at the caudal end of the weevil's abdomen. During the instant the ovipositor remains within the host abdomen an egg is placed freely in the haemocoele.

In the laboratory *M. aethiops* infrequently parasitized members of its own species. Eggs in various stages of development were dissected from the haemocoele of female and male parasites. One such egg had developed embryonically to the active stage with a normal trophamnion; other eggs were small and appeared abnormal. This parasitism occurred in cages with weevils, and presumably was accidental.

Often the ovipositor struck the elytra or pygidium of the host and failed to penetrate the haemocoele. This was demonstrated in tests with adults of *S. humeralis* and of *S. cylindricollis*. One female parasite was placed with 15 weevils of each species; oviposition attempts were recorded, and the weevils were then marked and dissected several weeks later. The number of strikes on individual weevils of either species varied between one and ten, and a total of 25 were made at nine *S. humeralis* and 23 at six *S. cylindricollis*. None, however, was parasitized. Thus the parasite may strike many times but not succeed in depositing an egg.

In the laboratory *M. aethiops* parasitized *S. cylindricollis*, *S. hispidula*, *S. scissifrons* (Say), *S. humeralis*, *S. puncticollis* (Steph.), *S. crinita*, *S. sulcifrons* (Thunb.), *Hypera postica*, *H. nigrirostris*, and *H. meles*. No oviposition preference between species of *Sitona* was evident from dissections. However, there was more parasitism and superparasitism of *S. cylindricollis* than of *H. meles*. Data are as follows:

Species	No. of weevils			Per cent parasitism	No. of parasites		
	Exposed	Dissected	Parasitized		Total	Mean per weevil	Range per weevil
S. cylindricollis	950	487	275	56.5	380	1.38	1–10
H. meles	430	193	52	26.9	54	1.03	1–2

Longevity of 17 females of *M. aethiops* (French strain) at 74° F. ranged from 6 to 17 days (mean 12.1 days). The male is somewhat shorter lived. The life-

span under cooler insectary condition was longer: that of 14 females ranged from 11 to 22 days (mean 16.9 days).

Development of the Immature Instars

The development of the egg is similar to that of *Pygostolus falcatus* (Loan and Holdaway, 1961). There is an increase in volume after deposition within the host and differentiation of the embryo and trophamnion. The expansion in microns of the egg of *M. aethiops* (French strain) in *S. cylindricollis* at 74° F. appeared as follows:

No. of eggs	Age in hours	Average length less pedicel	Average width	Average increase in size
10	ovarian	153	14	1.0
10	24	297	31	7X[1]
7	48	495	117	170X
5	72	585	113	187X
10	96	868	261	1473X

[1] $X =$ times mean ovarian size; volume calculated from $V = \dfrac{\pi B^2 A}{6}$,

B is the diameter and A the length of the egg.

The maximum size observed was 1058 μ long and 324 μ wide; this egg was 98 hours old including a two-hour period of exposure to the parasite. Its volume (less pedicel) relative to that of the average ovarian egg (less pedicel) increased about 2790 times. At 74° F. in *S. cylindricollis* and *S. lineata* the period from deposition of the egg to eclosion of the larva varied from 4 days, 19 hours, to 5 days, 1 hour. Hatching and dissociation of the cells of the trophamnion (Fig. 6a-c) was not unlike that of *Pygostolus falcatus*. The free cells, or teratocytes, are oblong to spherical and 18 by 31 μ to 23 by 45 μ in size. The trophamnion and embryo are enclosed by the chorion until eclosion. Supernumerary eggs were normal and developed to maturity. The larvae hatching from them died soon after eclosion; none was recovered alive.

The development of larval instars I to IV (Swedish strain) was completed in seven to eight days at 74° F. The period from egg deposition to emergence of the instar V larva was 12-13 days; at 65° F. it was 15-18 days; and at 80° F., 11-12 days. The stadia of the individual instars were estimated from the age of the larva and the number of cast skins at the tail of the larva. The development was rapid from one instar to the next when diapause of the instar I larva did not intervene. Larvae dissected eight and nine days after egg deposition were instar III because they carried casts of instars I and II and contained the developing, characteristic, cuticle of instar IV. Thus the stadia of instars I, II, and III are of short duration, probably about one day each. Instar IV larvae were recovered 8-12 days after deposition of the egg, a period of development of about four days. This instar, as with *Pygostolus falcatus*, is terminated by the instar V larva when it emerges from the weevil host.

The number of days from deposition of the egg to emergence of the instar V larva (French strain) at 74° F. ranged between 12 and 17 (mean 13.9), and to emergence of the adult, between 20 and 25. There was no apparent difference in the period of development in *H. meles* and *S. cylindricollis*, nor in the sex of the larva. Under widely variable insectary conditions the period of development in *H. meles* and *H. nigrirostris* from deposition of the egg to emergence of the adult

ranged from 28-35 days (immature stages within host, 22-26 days; cocoon stage, 6-9 days).

The instar V larva drops free of the weevil host. It immediately burrows between particles of soil and spins a cocoon. It also spun up readily on plastic, cloth, and wood floors of cages.

At 65° F. the adult parasite emerged from the cocoon in 10-14 days; at 74° F., 8-9 days; and at 80° F., 5-7 days (Swedish strain).

Effects of Parasitism

Emergence is effected through the caudal end of the weevil's abdomen where the membrane between the apical sternite and tergite is torn. After emergence of the larva the host weevil may walk about but does not feed and dies within one day. There were no apparent external signs of parasitism. The abdomens of some weevils, both parasitized and nonparasitized, were slightly distended. The internal effects of parasitism are similar to those described for *Pygostolus falcatus* (Loan and Holdaway, 1961). The haemocoele from which a parasite larva emerged is devoid of fluids and fat bodies; the intricate network of fat body tracheae is distinct (Figs. 10-11). Many host tracheae enmesh the larva in the later period of its development.

The effect of parasitism on oviposition of the female weevil was observed in *S. cylindricollis* collected on May 4, 1960, and parasitized on May 9. Before parasitism each female in successive 24-hour periods laid from 25.4 to 63.8 eggs at 74° F. On May 9, 10 of the 20 weevils were exposed to *M. aethiops* for 4 hours. On May 10 the number of eggs laid by these weevils was 4-22, and on May 11, 2 eggs only were recovered from one female. The weevils were dissected May 12-13, and each contained from 1-6 parasite eggs. The 10 weevils not exposed to *M. aethiops* continued to oviposit. A similar effect on reproduction was reported for *Pygostolus falcatus* (Loan and Holdaway, 1961). The degeneration of the ovaries, and the retention and shrinking of mature eggs described for that species is also effected by *M. aethiops*. Parasitism does not affect the potency of the male weevil.

Diapause

The development of many instar I larvae was arrested by diapause that occurred in a wide range of host species and in both overwintered and summer-emerged hosts. A similar diapause was reported for *Pygostolus falcatus* (Loan and Holdaway, 1961). The diapause larva is small (mean length 1433 μ), active, and the brain ganglia are not enlarged. Such larvae were found in dissections 7 to 100 days after parasitism. On the other hand, non-diapause larvae developed rapidly to the second instar one or two days after eclosion. The weevils were parasitized in May and June, as *M. aethiops* was available at that time from French cocoons. In the insectary in 1953 four instar V larvae emerged from 47 *H. meles* and four larvae from 18 *H. nigrirostris*, and none from 160 *S. cylindricollis*. Diapause larvae were found in the *Hypera* species six weeks after parasitism, but most of the larvae found in *S. cylindricollis* were dead. Comparable results were obtained in 1953 at 74° F. from 700 *S. cylindricollis*. In 1955, 950 *S. cylindricollis* and 430 *H. meles* were parasitized to determine the extent of development at 74° F. The emergence and dissection data are as follows:

| | No. of weevils with larvae | | |
Species of host	Emerged	In diapause	Dead
S. cylindricollis	34	39	231
H. meles	68	43	3

Fig. 10. *Sitona cylindricollis* after emergence of the parasite larva of *Microctonus aethiops*: the fat body has gone leaving the tracheae clearly evident; testes are prominent left of centre.

Fig. 11. Non-parasitized *Sitona cylindricollis* showing abundant fat body.

The low emergence of larvae from *S. cylindricollis* and the small proportion of diapause larvae was a result of mortality of the instar I larva, whereas the emergence from *H. meles* was affected chiefly by diapause. The parasite larvae at 74° F. and in the insectary remained in diapause as long as the overwintered weevils remained alive. Most of the latter died by August and the larvae perished with them. Thus the diapause of *M. aethiops* in overwintered weevils is an abnormal condition leading to the death of the larva. Diapause of larvae in summer-emerged weevils is a normal condition as such weevils overwinter and with them the instar I larva, which resumes development and completes larval growth in the spring or early summer.

Differential Mortality

The per cent mortality of instar I larvae in *H. meles* and *S. cylindricollis* in 1955 was compared by the t test (Cox, 1954) and the difference between them was significant at the one per cent level.

The incidence of mortality in *S. humeralis*, *S. scissifrons*, and *S. cylindricollis* was determined in 1956. The weevils were dissected live, five days or more after exposure to the parasites. Living and dead larvae were obtained as follows: *S. humeralis*, 15 instar I larvae, 13.3 per cent (2) dead; *S. scissifrons*, 16 instar I larvae (none dead); *S. cylindricollis*, 50 instar I larvae, 58 per cent (29) dead. The difference in per cent mortality between *S. cylindricollis* and *S. humeralis*, and between *S. cylindricollis* and *S. scissifrons* was significant at the one per cent level. Survival in *S. cylindricollis* was higher in 1956 than in 1955. There was, however, an interval of about five weeks between parasitism and preservation of the live weevils in 1955. In 1956 the parasite larvae were dissected at the time of eclosion, and some of those found alive might have died later.

Dead larvae in *S. cylindricollis* (Fig. 12a-g) were found from the sixth day after deposition of the egg, i.e. the first or second day after eclosion. Many were less than 500 μ long with faintly sclerotized head capsule and clear mid-gut. This appearance suggests that they died soon after eclosion. Other larvae were 525 to 840 μ long: the abdomen was not caudate but shrivelled and flaccid, and often only the head capsule was discernible. Small areas of melanin existed on some larvae between the segments of the abdomen, between the head capsule and thorax, and on the head capsule. Loose aggregations of haemocytes partially surrounded many larvae. These structures were incomplete and slipped away from the larva with slight pressure of a dissection needle. Dead larvae normal in appearance (Fig. 12f) were also found; their length and the yellow mid-gut suggested that they had remained alive for some time after eclosion. One living larva (Fig. 12g) was recovered with a band of discrete, black melanin encircling the prothorax next to the head capsule, which was surrounded by a mass of haemocytes.

Dead larvae in *H. meles* differed from larvae observed in *S. cylindricollis*. They were completely melanized, stiff, greatly reduced in size, and difficult to recognize.

Perilitus rutilus (Nees)

Descriptions

Jackson (1928) described in detail the egg stage, but descriptions of the larval instars have not been published. Large numbers of weevils were parasitized to obtain larvae for this purpose. However, diapause of the instar I larva interrupted development, and data were obtained on the penultimate and final instars only. The five larval instars are very similar to those of *M. aethiops*. A single
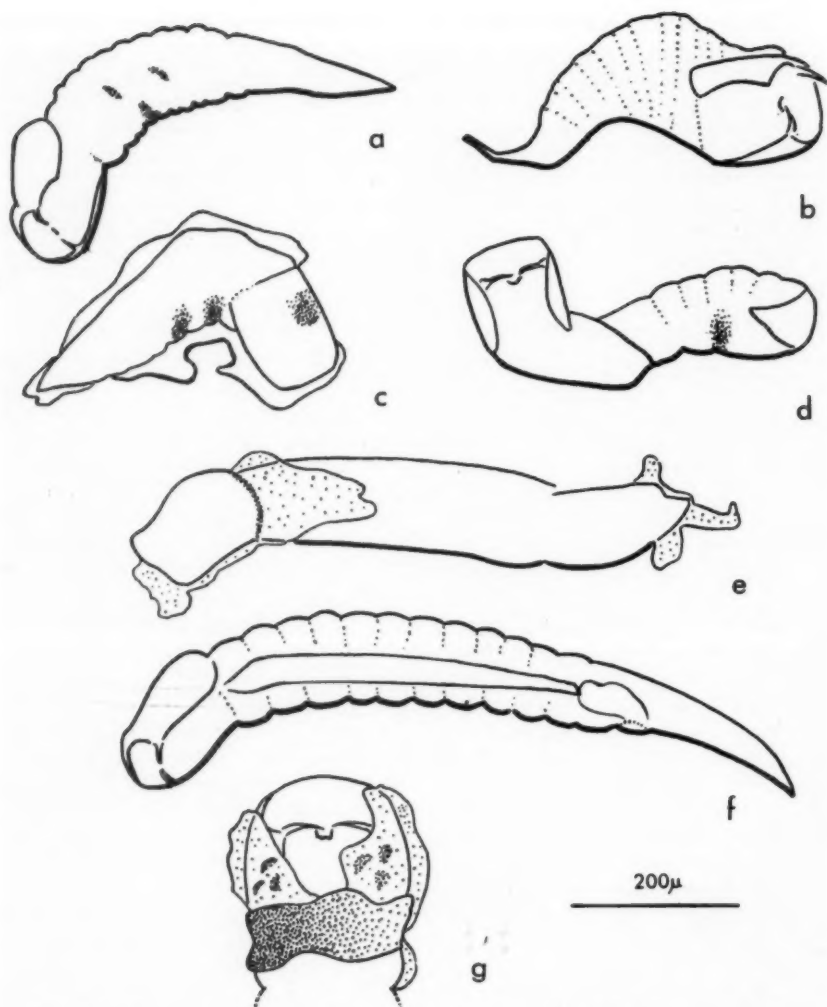
Fig. 12. *Microctonus aethiops*. Host reaction in *Sitona cylindricollis*. a-e, dead instar I larvae 8-11 days old, slightly melanized or with loose aggregations of haemocytes; f, dead larva 22 days old without melanization or haemocytes; g, live instar I larva 15 days old with discrete band of melanization around the head and prothorax, spotting of the head capsule with melanin, and masses of haemocytes.

character, the hypostomal spur of the stipital sclerite, separates the instar V larvae.

Egg

The ovarian egg (Fig. 14a)is similar in form to that of *M. aethiops* but is wider. The length is variable: including the pedicel, that of one female 207-252 (233) μ, and of a second female 180-216 (208) μ; the pedicel itself ranged from 50-68 (59) μ and from 68-95 (86) μ respectively. The width of 20 eggs was about 54 μ.
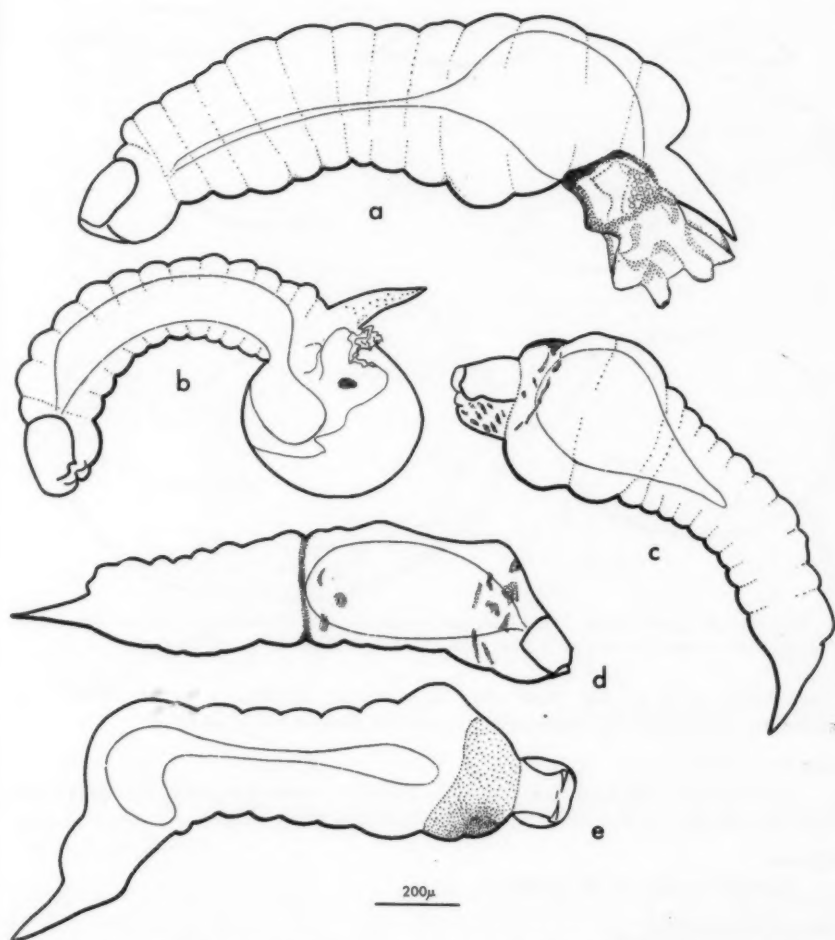
Fig. 13. *Microctonus aethiops.* Host reaction in *Sitona cylindricollis,* abnormal mature instar I larvae 21-23 days old.

The shape of the egg as it develops and increases in volume after deposition is shown in Fig. 14b-g.   The mature egg is oblong to spherical, and its maximum size at 74° F. was 765 μ long by 576 μ wide in *S. cylindricollis.*   Jackson reported a mature egg 900 μ long by 520 μ wide.

Instar I Larva

Caudate, head capsule light stramineous in colour, cuticle smooth, tail with minute setae.   It is characteristic of this instar and of this species, to retain shreds of chorion around the thorax or abdomen.

Instar IV Larva

Larva (Fig. 15a) grub-like, whitish-yellow; length 2800-3619 μ; cuticle of head unsclerotized, faint lines suggest labial sclerite and hypostoma; mandibles
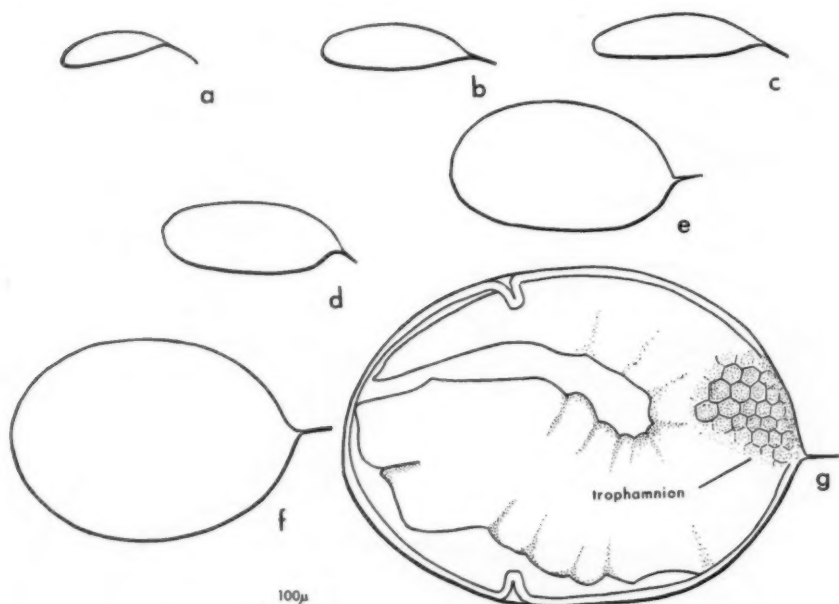
Fig. 14. *Perilitus rutilus*. Development of the egg. a, ovarian egg; b, one day old; c, two days old; d, three days old; e, four days old; f, five days old; g, six days old.

sclerotized, 36-58 μ long from apex to posterior of basal structure; cuticle of abdomen sculptured by brush-like microsetae similar to *M. aethiops*.

Instar V Larva

Larva (Fig. 15b-d) differs from *M. aethiops* in one consistent character: the hypostomal spur of *P. rutilus* is more pronounced (Fig. 16).

Cocoon

Similar to that of *M. aethiops*.

Adult and Ovaries

Marshall (1887) described the adult of *P. rutilus* and Jackson (1928) discussed the variation in colour and size of the male and female. The ovaries consist of a variable, unequal number of ovarioles (5-7) with young and fully formed oöcytes. The number of oöcytes per ovariole in six females 9-13 days old that had been placed with weevils from emergence of the parasites varied from 3-12, and per female, from 43-132.

Biology

Reproduction, Parasitism and Longevity

Jackson (1928) discussed the reproduction of *P. rutilus* and described the mating and oviposition behaviour. As in *M. aethiops*, mated females produce male and female offspring in more or less equal ratio, and only males result from arrhenotokous reproduction. One pair was seen to copulate for 55 seconds.

There was no apparent preference for *S. cylindricollis*, *S. scissifrons*, *S. hispidula*, or *S. lineata* as hosts. The weevils are trailed and parasitized throughout the day and at night. The parasitism and fecundity of two females that
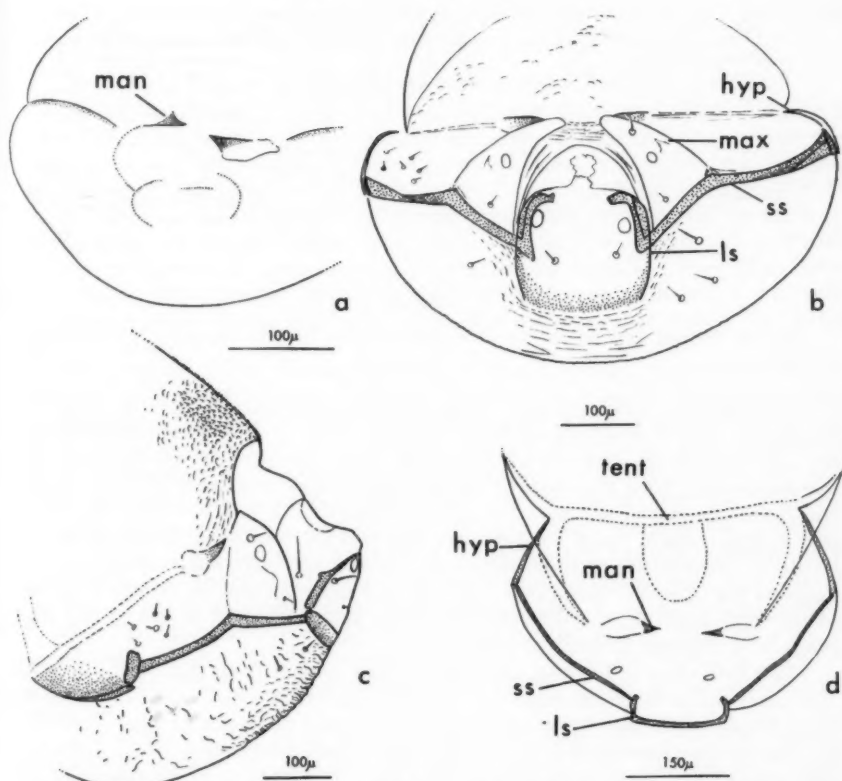
Fig. 15. *Perilitus rutilus*. The head of larval instars IV and V. a, anterior view of instar IV larva; b, anterior view of instar V larva; c, lateral view of instar V larva; d, dorsal view of instar V larva.

were supplied with ten weevils each at successive 24-hour intervals were studied in the insectary in June, 1959. One female parasitized 27 of 110 weevils and laid 45 eggs in 11 days, or a mean of 1.6 eggs per weevil. The second parasitized 29 of 110 weevils and laid 50 eggs in the same period; the average number of eggs per weevil was 1.7. Not more than one-half of the weevils available each day to either parasite was parasitized although superparasitism occurred.

The longevity of mated females in the insectary in June, 1959, varied from 24 hours to 17 days. At 74° F. males and females lived about two weeks; one female lived 33 days.

Development of the Immature Instars

Seven and eight days after oviposition, mature eggs were recovered from the host, and instar I larvae free or in the process of eclosion, six and seven days after egg-deposition. The duration of the egg stage is influenced by supernumerary eggs or larvae; an apparently normal egg sometimes does not hatch in the presence of another, or of an instar I larva. The hatching supernumerary larvae were motionless or slightly active and were surrounded by the freely-dissociating trophamnion, and to a lesser or greater extent, by the chorion. Instar I larvae in diapause were found throughout the period of dissection.
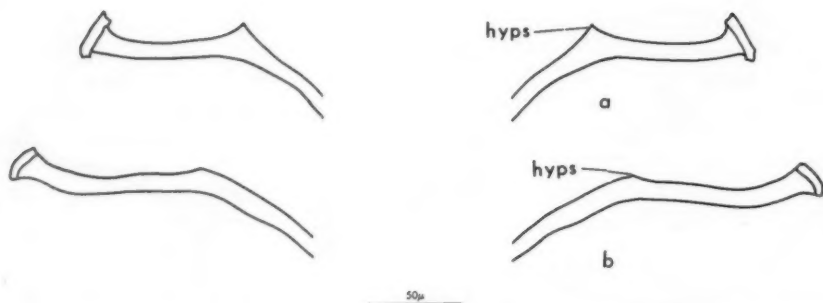
Fig. 16. Stipital sclerites. a, *Perilitus rutilus*: hyps, hypostomal spur; b, *Microctonus aethiops*.

The period of development of the non-diapause instar I larva was not determined. The first advanced larva was recovered 11 days after deposition of the egg and others after 13-17 days; the latter larvae were enclosed by the transparent cuticle of the instar IV larva. Larvae showing the sclerotized stipital and labial sclerites of the final instar were dissected 15-18 days after deposition of the eggs. Such larvae were mature and probably ready to emerge from the weevil. The sclerites of some larvae of a similar age were not evident, and this suggests that sclerotization occurs rapidly at a certain point in the development of the final instar larva. The cuticle of the instar IV larva is cast as the final instar larva emerges from the weevil.

The behaviour of the final instar larva is not distinct from that of *M. aethiops*. The larva drops from the host weevil and crawls with a backward locomotion. On a flat surface it may travel aimlessly, fail to spin a cocoon, and die. Mortality for this reason exceeded 60 per cent in cages where no crevices or folded cloth were provided. No mortality occurred when the larva spun up in soil. Cocoon formation was completed in about 12 hours at 74° F. The adult emerged 9-14 days later.

Effects of Parasitism

The weevil is killed by the emergence of the larva. The internal effects of parasitism are similar to those in *M. aethiops*. According to Jackson (1924) the ovaries are "rendered functionless" and "eggs already present degenerate". Some weevils were dissected with the ovaries in this condition; others containing instar IV larvae appeared normal, although none was gravid.

Diapause

Instar I larvae were affected by a diapause similar to that of *M. aethiops*. Many larvae failed to develop in overwintered weevils, and none in summer-emerged ones. Mortality of larvae, however, was low: 2.4 per cent (3) in *S. cylindricollis*, and 11.5 per cent (6) in *S. lineata*.

In overwintered *S. cylindricollis*, 97. 5 per cent (77) and in *S. lineata* 77.3 per cent (34) of live larvae were in diapause at 74° F. in July, 1956. The larvae were progeny of Swedish *P. rutilus* reared at Belleville in June from *S. lineata*. Summer-emerged *S. cylindricollis*, *S. hispidula*, and *S. lepidus* Gyll. were parasitized in 1958 and 1959 but no larvae emerged at 74° F. or in field cages from August to the onset of winter. The diapause of *P. rutilus* larvae at 74° F. in summer-emerged *S. cylindricollis* was terminated by a period of 67 days at 46° F. One hundred weevils placed at this temperature on August 20, 1959, and removed

to 74° F. October 26, produced 26 larvae from November 2 to 13. No parasite larvae in diapause was found in the remaining weevils.

Field History of *Microctonus aethiops* and *Perilitus rutilus*

Berry and Parker (1950) listed the species of *Sitona* and *Hypera* swept in mass collections in Europe for parasite rearings. *S. humeralis* and *H. postica* predominated in the collections from France examined at Belleville and no doubt are the major host species of *M. aethiops* and *P. rutilus*. *S. lineata* was the dominant weevil species in Swedish collections from 1956 to 1960, and the majority of *P. rutilus* was reared from it, whereas *M. aethiops* emerged from *S. hispidula*. The weevils generally overwinter as summer-emerged adults. However, Markkula (1959) found that in Finland a small proportion of *S. lineata, S. hispidula*, and several other species may live in the adult stage for two years, thus hibernating twice.

M. aethiops and *P. rutilus* overwinter in France as instar I larvae in summer-emerged weevils. Emergence of larvae of *M. aethiops* occurs during late April and early May, and the cocoons formed were used in biological control attempts in North America. The larvae are probably the progeny of the overwintered parasite generation but some of them may be overwintered larvae developing from diapause. The parasite adults emerge in France in May and June and parasitize summer-emerged weevils, and probably overwintered ones when present. Parker (*in litt.*) suggested that *H. postica* is attacked first, the parasitism later shifting to *Sitona* spp. In June, 1957, in France, five per cent of *S. humeralis* and 16 per cent of *H. postica* were parasitized by *M. aethiops* (and possibly *P. rutilus* as the instar I larvae are identical). This difference, however, may be correlated with the greater abundance of *H. postica* in June: in July, when *S. humeralis* was abundant, the incidence of parasitism of both species was five per cent.

The instar I larvae of *M. aethiops* are in diapause as early as June, and the majority of them do not develop until the following year. Five larvae emerged at Belleville from 14,226 of the summer-emerged *S. humeralis* (including small numbers of lesser species) and 5,000 *H. postica* in 1956 and 1957; the weevils were held at 74° F. for emergence. Of these totals, 4,500 *S. humeralis* and 1,500 *H. postica* were collected in June and July, 1957, and held by Dr. Parker until October for parasite emergence. In this interval three larvae of *M. aethiops* emerged, and in late October at Belleville, a single larva of *M. aethiops*. The parasitism in 1956 and 1957 collections varied from 4 to 16 per cent.

M. aethiops was reared only from fall Swedish collections of *S. hispidula* in 1956 and 1957. None emerged from extensive spring and summer collections during 1957 to 1959. The species overwintered as diapause instar I larvae at Ivanhoe, Ontario, within *S. cylindricollis* as two males emerged in May, 1957. The minimum air temperature recorded near the hibernation site was −36° F.

Summary

Microctonus aethiops (Nees) auctt. and *Perilitus rutilus* (Nees) are endoparasitic braconids of the subfamily Euphorinae. They parasitize adult weevils of the genera *Sitona* and *Hypera*. *M. aethiops* was reared at Belleville from *S. humeralis* Steph., *S. crinita* Hbst. (= *macularia* Marsh.) and *H. postica* Gyll. from France, and *S. hispidula* (F.) from Sweden; *P. rutilus* was reared from *S. humeralis* from France and from *S. lineata* (L.) from Sweden. The life history and immature stages of *M. aethiops* and *P. rutilus* were studied as a prerequisite to their release in North America as biotic agents of the sweetclover weevil, *S. cylindricollis* Fahr.

M. aethiops and *P. rutilus* emerged with ripe oöcytes enclosed in a variable number of ovarioles. Mated females produce male and female progeny: the sex ratio of *P. rutilus* reared from Swedish weevils was about equal, whereas slightly more females than males of *M. aethiops* emerged from French cocoons. Virgin females produced male progeny only. *M. aethiops* parasitized species of *Sitona* without discrimination, but a preference was indicated for *S. cylindricollis* over *H. meles* (F.).

Eggs of both parasite species are deposited in the haemocoele at the caudal end of the weevil's abdomen. Within four days of deposition that of *M. aethiops* increased from the ovarian average of 153 μ long (less pedicel) and 14 μ wide to a maximum of 1058 μ long and 324 μ wide; that of *P. rutilus*, within seven days of deposition, from the ovarian average of 143 μ long (less pedicel) and 54 μ wide to 765 μ long and 576 μ wide. At eclosion the cells of the trophamnion dissociate as free cells (teratocytes). One larva only develops or remains alive in a weevil: the supernumeraries of *M. aethiops* died soon after eclosion, and those of *P. rutilus*, as mature eggs or hatching larvae. Five larval instars were determined; those of *M. aethiops* are described. The approximate periods of development in days of *M. aethiops* at 74° F. were: egg, 4-5; larval stages 8-9: instars I-III, 1 day each; instar IV, 4; instar V, 1; pupa, 8-9. Similar data of *P. rutilus* are: egg, 6-7; larval stages, 9-12; pupa, 9-14. The instar V larva of both species is enclosed by the cuticle of the penultimate larva until emergence from the host. The development of many instar I larvae is arrested by diapause in overwintered and summer-emerged weevils. Many instar I larvae of *M. aethiops* from France died in *S. cylindricollis*; few or none died in *H. meles*, *S. humeralis*, and *S. scissifrons* Say, and low emergence of final instar larvae was due to diapause. On the other hand, survival of *M. aethiops* from Sweden was normal in *S. cylindricollis*, suggesting biological differences between the French and Swedish forms of *M. aethiops*.

M. aethiops and *P. rutilus* overwinter as instar I larvae within summer-emerged weevils. Their combined parasitism in France has not exceeded 16 per cent; in Sweden, that of *P. rutilus* has varied from 4.0 to 12.2 per cent.

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Influence of Various Foods on Fecundity and Longevity of Adults of *Scambus buolianae* (Htg.) (Hymenoptera: Ichneumonidae)

By K. Leius

Entomology Research Institute for Biological Control, Research Branch
Canada Department of Agriculture, Belleville, Ontario

Introduction

The effects of food on the fecundity and longevity of the adults of hymenopterous parasites vary remarkably, not only between species that are host feeders and those that are not host feeders, but also within these groups. It is known, for example, that the females of *Itoplectis conquisitor* (Say) develop only few eggs without feeding on body fluids of their host. In the present investigations it is shown that the females of *Scambus buolianae* (Htg.) are not able to deposit any eggs without first feeding on the tissues of their host. Such information is important for the successful establishment of newly-imported parasites.

According to Thorpe (1930), Thompson (1957), and several others, *S. buolianae* has been recorded only from the European pine shoot moth, *Rhyacionia buoliana* (Schiff.). The preliminary tests conducted in the laboratory show that females of *S. buolianae* punctured, killed, oviposited on, and consumed not only this host but also larvae of the imported pine budworm, *Exoteleia dodecella* (L.), and the following native Canadian species: eastern tent caterpillar, *Malacosoma americanum* (F.); ugly-nest caterpillar, *Archips cerasivoranus* (Fitch); and spruce budworm, *Choristoneura fumiferana* (Clem.). The immature stages of *S. buolianae* were also reared successfully on all these hosts. In laboratory tests the females did not parasitize or consume any of the following larvae: the red humped caterpillar, *Schizura concinna* (J. E. Smith); older instars of the orange-

striped oakworm, *Anisota senatoria* (J. E. Smith); the Essex skipper butterfly, *Thymelicus lineola* (Ochs.); the fall webworm, *Hyphantria cunea* (Drury); the cinnabar moth, *Hypocrita jacobaeae* (L.); the red-headed pine sawfly, *Neodiprion lecontei* (Fitch); the goldenrod beetle, *Trirhabda canadensis* (Kby.); or the aphid, *Aphis nasturtii* (Kalt.).

Coddled larvae of the greater wax moth, *Galleria mellonella* (L.), were successfully used in experiments for oviposition, as food for female adults, and for the rearing of immature stages. Though the females of *S. buolianae* rejected coddled or living larvae of *N. lecontei* for ovipositing and feeding, parasite eggs transplanted from wax moth larvae onto coddled sawfly larvae that had been removed from their cocoons developed normally and were successfully reared to the adult stage.

These data show that *S. buolianae* is not a specific parasite of *R. buoliana*, because it can parasitize several other orchard and forest pests. Furthermore these investigations show that *S. buolianae* apparently can parasitize such hosts as *E. dodecella* and *C. fumiferana*, which were recorded by Walley (1960) for *Scambus tecumseh* Vier., so that these two species are not only morphologically, but also ecologically, similar.

Previous Work

S. buolianae, an external larval parasite of the European pine shoot moth, *R. buoliana*, was introduced into Canada in 1956 (Arthur and Juillet, 1961). It is not yet known to be established but may have been overlooked because of its close similarity to the native *S. tecumseh* that, according to Walley (1960), may not be a distinct species.

There is little information about the feeding habits of *S. buolianae* adults other than that in a previous paper by Leius (1960). He found that the females usually did not feed on the day of emergence; on the second day they began feeding on carbohydrate foods for two to six days. Then the females started to feed on body fluids of the host, in addition to carbohydrates, and this type of feeding normally continued until death. Leius (1960) also showed that the males of *S. buolianae* were not attracted to host larvae, probably because they did not feed on body fluids of the host. Leius (1960) found that diluted honey attracted about three times as many females as sucrose solution, pollen in sucrose solution, or honeydew of aphids. He also found that the adults of *S. buolianae*, though preferring umbelliferous flowers, were attracted to some extent to other flowers.

Materials and Methods

Eleven diets were tested using 10 females and 10 males in each of two cages, making a total of 22 cages. The diets without host protein were: (1) 37.5 per cent (by weight) sucrose solution, (2) 1 per cent (by volume) Scots pine pollen in 37.5 per cent sucrose solution, (3) diluted honey with approximately 37.5 per cent (dry weight of honey) sugar content, (4) honeydew exuded by the aphid, *A. nasturtii*, on potted potato plants, (5) honeydew exuded by the aphid, *Myzocallis alhambra* Davids., on leaves of bur oak, (6) distilled water. Diets number 7 to 11 were the same as the above, except for number 5, but host protein was provided by the addition of coddled wax moth larvae.

Adults of *S. buolianae* were reared in the laboratory and fed a 50 per cent aqueous solution of honey and water to which was added 1 per cent (by volume) of birch pollen. Mature larvae of *G. mellonella* coddled for 45 seconds in running water at 130°F. were provided as hosts. Eggs deposited on wax moth larvae were transplanted and the immature stages reared on cocooned larvae of

N. lecontei coddled for 90 seconds in running water at 130°F. The unpigmented parasite pupae were stored in a cold room (about 36°F.) to obtain a uniform emergence. About 10 days before the experiment all pupae were taken out of cold storage and kept three days at 42°F., three days at 65°F., and then at 76°F. until the pupae completed development and the adults emerged.

The honey and sucrose were dissolved in distilled water. The pollen was fed as a suspension in the sucrose solution. All liquid foods were provided in cages on ¾″ lengths of dental cotton, except the honeydew which was supplied by placing aphid-infested plants or leaves in the cages. To avoid differences in the nutritive value of the food substances, sufficient uniform supplies of honey, sucrose, and pollen were obtained prior to the experiment to last its duration. The pollen was hand-collected from Scots pine, *Pinus sylvestris* L., and air dried. Scots pine pollen was selected not because of its high nutritive value, but because it was easily available in large quantity. The wax moth larvae and all other foods, except the honeydew exuded by aphids on potato plants in the test cages, were renewed daily. Coddled wax moth larvae were placed in hollowed-out Scots pine twigs each with a narrow longitudinal slot on top. In each cage where the diet was without host protein, four wax moth larvae were placed in the hollowed twigs and covered with a double layer of plastic screen so that the females could oviposit in these but not feed on them. In cages where wax moth larvae were part of the diet, four larvae were covered with plastic screen and four larvae were provided in uncovered pine twigs. This was done because preliminary tests showed that the females preferred to lay the eggs on screened larvae.

Adults were placed in standard test cages (15″ x 8¾″ x 8¾″) on the day of emergence. The experiment lasted from the time the adults emerged until all insects in test cages died. The numbers of eggs deposited on wax moth larvae during the previous 24 hours were recorded every morning. Daily records on the mortality of the adults were also maintained. The experiment was conducted in the laboratory at a temperature of 76 ± 1°F. and a relative humidity of 66 ± 1 per cent.

Analyses of variance and Duncan's multiple range test (Duncan, 1955) were applied to the data to test the significance of the differences between both fecundity and longevity of adults on the different diets. Results were analyzed for each sex separately, and estimates of the error variance were obtained from differences between duplicate cages. All the comparisons were analyzed at the one and five per cent levels. In descriptions of results significance is given at one per cent level unless otherwise stated.

Results and Discussions

Feeding Habits of the Adults

To obtain more fluid from a larva, the female, after piercing the cuticle, enlarged the puncture hole with her mandible, and ate the hemolymph that filled the excavation (Fig. 1). The female did not eat the whole larva unless it was very small, such as that of *E. dodecella* or the younger larvae of other Lepidoptera. This indicates that the females normally feed on body fluids of the host but sometimes consume other tissues. The females usually fed daily on the host fluids, stopping this feeding only on the day of their death.

The females also fed on carbohydrate foods, with or without pollen, in addition to body fluids of the host. It seems that the quantity and value of carbohydrates and other nutrients found in the body fluids of the host is not adequate for normal life of the adult parasites, so they must obtain additional sources of food. The males only feed on carbohydrate food (with or without pollen).
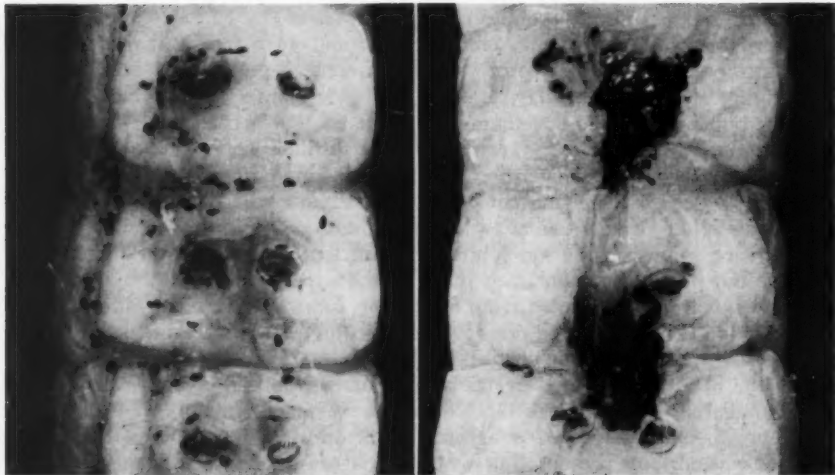
Fig. 1. Greater wax moth, *Galleria mellonella*, larvae attacked by the females of *Scambus buolianae*: (left) puncture wounds, (right) wounds caused by feeding.

They were not attracted to host larvae and were never observed to feed on fluids of the host exuding from excavations made by females in the same cage.

Influence of Food on Fecundity

The results of this experiment (Fig. 2, A) show that the females did not oviposit when body fluids of the host were not present in the diets (Foods 1, 2, 3, 4, 5, and 6). The greatest mean number of eggs per female was obtained when females were supplied with wax moth larvae plus pollen in sucrose solution (Food 8). Females that had access to larvae-sucrose solution but not to pollen (Food 7) laid significantly fewer eggs, thus indicating that the addition of pollen to sucrose solution increased fecundity. The females supplied with larvae-honey (Food 9) deposited fewer eggs than those fed larvae-pollen-sucrose, but significantly more than those in cages where the females were supplied with larvae-sucrose but not pollen. In cages where the females had access only to body fluids of the host without additional carbohydrates (Food 11), the mean number of eggs per female was significantly less than in cages where host fluids and carbohydrates were combined. On the average, only a few eggs per female were deposited in the cages where the females could feed on honeydew exuded by the aphid *A. nasturtii*, as well as on body fluids of the host (Food 10). This indicates that this honeydew may have undesirable physical properties; possibly one of the oligosaccharides, namely melezitose, found in honeydew is as detrimental to the adults of *S. buolianae* as it is to those of *I. conquisitor* (Leius, 1961).

Influence of Food on Longevity

Females.—The results of this experiment (Fig. 2, B) show that specimens fed on the larvae-pollen-sucrose diet (Food 8) lived significantly longer than those fed on any other diet in the experiment, thus showing that the addition of pollen not only increased fecundity but also longevity (Food 8 vs. 7). Diluted honey (Food 9), with its small pollen content, did not lead to any appreciable increase in the longevity of the females (Food 9 vs. 7, $P > 0.05$). When the females were supplied only with body fluids of the host (Food 11), their lives were shorter
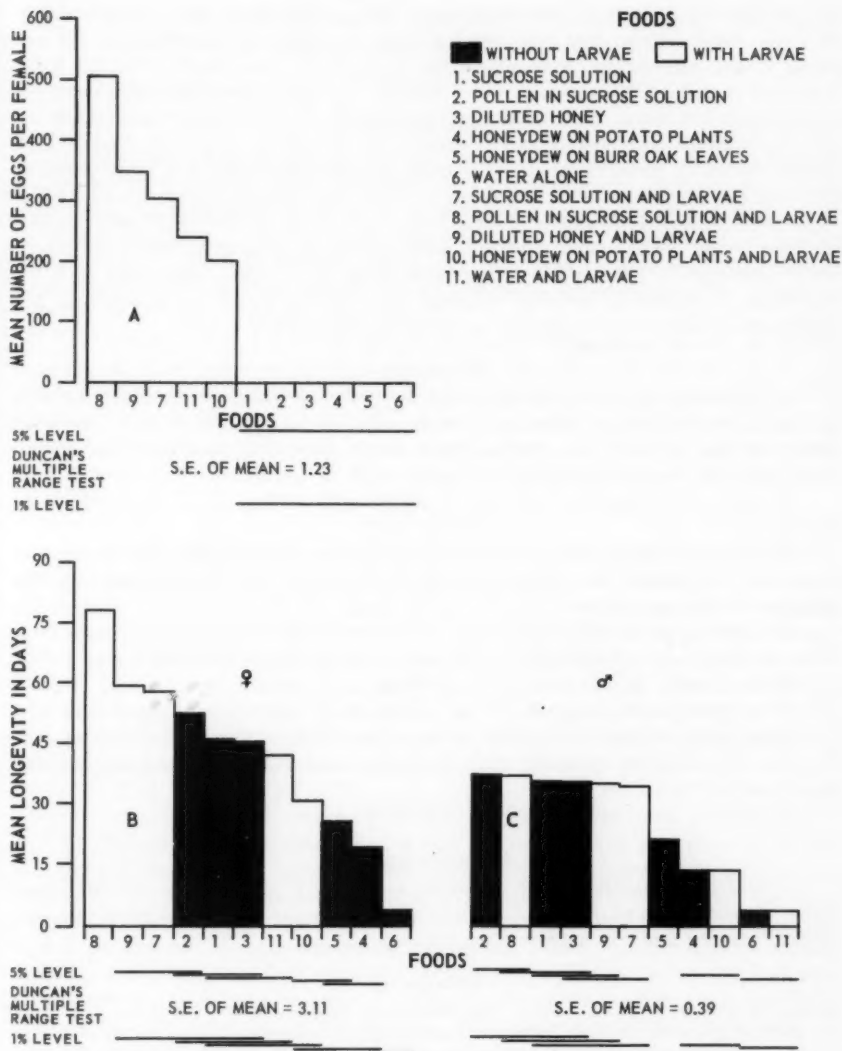
Fig. 2. A comparison of the influence of food on the fecundity and longevity of the adults of *Scambus buolianae*: A — fecundity of the females, B — longevity of the females, C — longevity of the males. The means for the foods that are underscored by the same line are not significantly different at the 5 per cent level (top lines) or the 1 per cent level (bottom lines).

(P < 0.05) than when carbohydrates were also supplied. There was no difference in length of life of the females fed only on host fluids and those that received only carbohydrates (Foods 11 vs. 1 and 3), but the food value of pollen was superior (P < 0.05) to the host fluids (Food 11 vs. 2). Females supplied with water or honeydew alone died sooner than on any other diet in the experiment.

Males.—The results of this experiment (Fig. 2, C) show that the availability of body fluids of the host that exudes from wounds made by females did not result in any increase in longevity of the males in the same cages (Food 1 vs. 7, 2 vs. 8, 3 vs. 9, 4 vs. 10, and 6 vs. 11). Indeed, in cages where the males were fed sucrose solution alone, they lived significantly ($P > 0.05$) longer than those fed sucrose solution and host larvae (Foods 1 vs. 7). This might, of course, be a chance effect, or perhaps some of the males accidentally consumed body fluids of the host as strange food and died sooner. The males supplied with the two types of honeydew had significantly shorter lives than those supplied with other carbo-hydrate foods. The males supplied with pollen in sucrose solution (Food 2) lived significantly ($P > 0.05$) longer than those fed on any other diet with the exception of pollen in sucrose solution and larvae (Food 8) which was not significantly different in value ($P > 0.05$) from Food 2.

Summary

In laboratory experiments the females of *Scambus buolianae* attacked not only the larvae of the European pine shoot moth, *Rhyacionia buoliana*, its only recorded host, but also several other orchard and forest pests. *S. buolianae* was reared successfully to the adult stage on the larvae of these hosts.

Females of *S. buolianae* did not oviposit without feeding on body fluids of the host.

The greatest mean number of eggs per female was obtained when the females were fed host larvae plus pollen in sucrose solution. The females kept on this diet also lived longer than those fed other foods.

Females supplied with host larvae alone deposited fewer eggs and their lives were shorter than those supplied with both carbohydrates and host larvae.

Males usually did not feed on body fluids of the host.

The presence of pollen in the diet of the males slightly prolonged their life.

Honeydew exuded by *Aphis nasturtii* and *Myzocallis alhambra* was det-rimental for females, reducing their fecundity and longevity, and was also an unsatisfactory food for males.

Both sexes lived only a few days on water alone.

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Etude sur la mouche-à-scie du peuplier, *Trichiocampus viminalis* (Fall.) (Hyménoptère: Tenthredinidae)[1]

RENÉ BÉIQUE[2]

Introduction

La distribution géographique circompolaire et très étendue de la mouche à scie du peuplier comprend toute l'Europe et la partie septentrionale de l'Amérique du Nord. Au Canada on a signalé sa présence de l'Atlantique au Pacifique.

Dans le Québec, cet insecte n'avait jamais été signalé comme très nuisible avant 1956, alors qu'il se multiplia soudainement d'une façon excessive occasionnant des défoliations importantes sur les peupliers ornementaux, dans certains secteurs de la ville de Québec.

Cet insecte a fait l'objet de quelques travaux importants, parmi lesquels il importe de citer ceux de Della Beffa (1954) en Italie, de Fisher (1922) en Angleterre et de Downes (1925) au Canada. Mais il restait de nombreux points à préciser concernant son comportement sur ce continent, de même que sur les facteurs naturels susceptibles de limiter sa pullulation. C'est ce qui nous a incités à entreprendre une étude à son sujet que l'on trouvera résumée dans les pages suivantes.

Systématique

Trichiocampus viminalis, décrit par Fallén en 1808, appartient à la famille des Tenthredinidae, sous-famille des Nematinae, tribu des Cladiini. Lors de sa découverte en Amérique du Nord en 1888, Lintner crut voir une espèce nouvelle qu'il signala sous le nom d'*Aulacomerus lutescens* Lint. De son côté MacGillivray décrivit en 1920 sous le nom de *Platycampus victoria* MacG. des spécimens récoltés au Canada quelques années auparavant. Enfin, en 1925, Viereck démontra que les individus rencontrés en Amérique du Nord appartenaient bien à l'espèce *T. viminalis*. Il convient de mentionner le fait que certains auteurs européens ont déjà rangé cette espèce dans le genre *Cladius* (Barbey, 1913).

Hôtes

T. viminalis semble strictement inféodé aux peupliers et sa présence, maintes fois signalée sur le saule, résulte vraisemblablement de sa forte ressemblance avec une espèce voisine dans la classification, *T. irregularis* (Dyar) qui vit sur cette dernière essence. Dans la nature, nous ne l'avons jamais rencontré sur aucune espèce de saules. Nous avons réussi cependant à faire pondre quelques rares femelles et à obtenir le développement complet de quelques larves sur le *S. discolor*, une espèce à long pétiole. La plupart des autres espèces de saules de la région ont apparemment un pétiole trop court pour permettre à la femelle de déposer ses oeufs.

Toutes les espèces de peupliers que l'on trouve dans le Québec peuvent être attaquées par cette mouche à scie. Nous l'avons récoltée sur *Populus alba* L. probablement de la variété *nivea* Willd., *P. x euramericana* (Dode) Guinier cv. *eugenei*, *P. deltoides* Marsh., *P. balsamifera* L., *P. grandidentata* Michx., *P. tremuloides*, Michx., *P. tremula* L. x *tremuloides* Michx., et *P. nigra* L.

Parmi toutes ces essences, *P. nigra* est la plus fréquemment recherchée par l'insecte dans le Québec et elle héberge toujours les plus fortes populations. Toutefois, à défaut de cet hôte préféré, l'insecte s'accommode fort bien de plusieurs autres espèces de peupliers qu'il peut à l'occasion complètement défolier, tels que *P. tremuloides*, *P. balsamifera* et *P. grandidentata*.
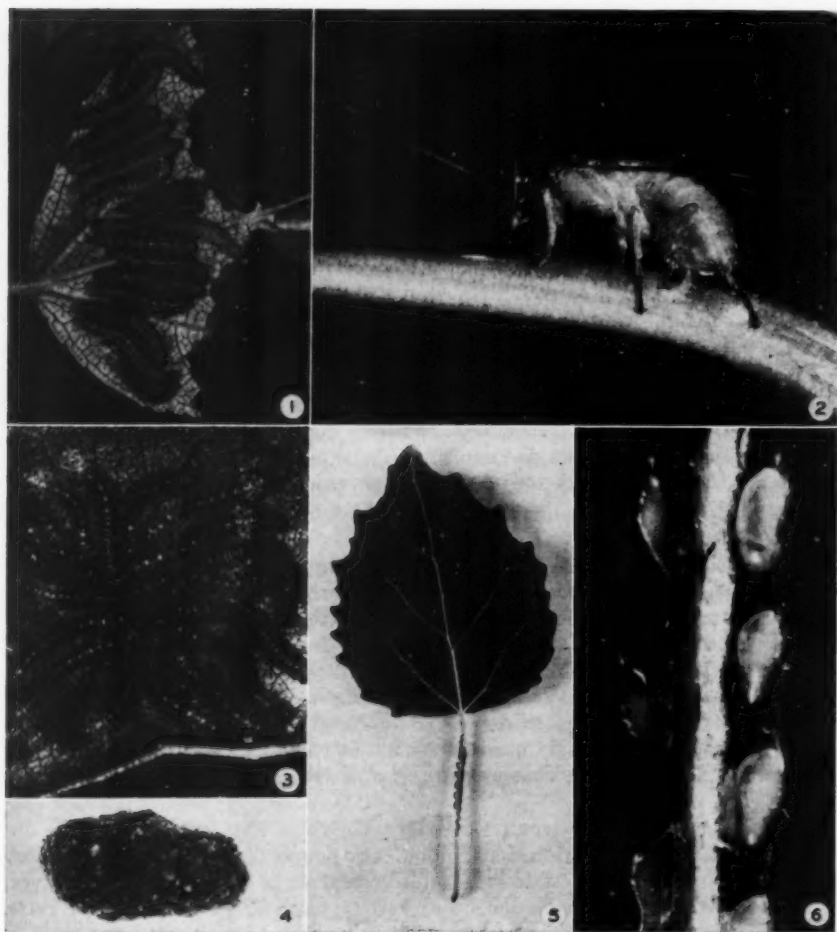
Figs. 1-6. 1. Larves adultes en position parallèle. 2. Femelle en train de pondre. 3. Larves au 4e âge disposées en rosette. 4. Cocon. 5. Série d'oeufs sur pétiole d'une feuille de peuplier. 6. Oeufs grossis dans leurs alvéoles.

Morphologie

Adulte: L'imago est de forme robuste (Fig. 1), les mâles mesurant environ 7 mm. de largeur sur 14 mm. d'envergure, les femelles 11 mm. de longueur sur 17 mm. d'envergure. La tête et le dessus du thorax sont noirs, tandis que le dessous du thorax, l'abdomen et les pattes sont jaune orangé. Le mésosternum est orné de deux taches noires contigues, en forme de triangle, juste à l'avant des coxae. Les ailes antérieures sont légèrement enfumées sur les deux-tiers proximal de leur longueur.

Oeuf: L'oeuf a une forme ellipsoidale, une couleur crème et mesure 1.36 ± 0.8 mm. de longueur sur 0.46 ± 0.7 mm. de largeur. Le chorion très fragile, est lisse et sans ornementation apparente. Une fois introduit dans le pétiole, l'oeuf s'applatit latéralement pour prendre la forme de l'alvéole qui le contient. Les oeufs sur le pétiole forment toute une série de petites boursouflures (Figs. 2 et 3).
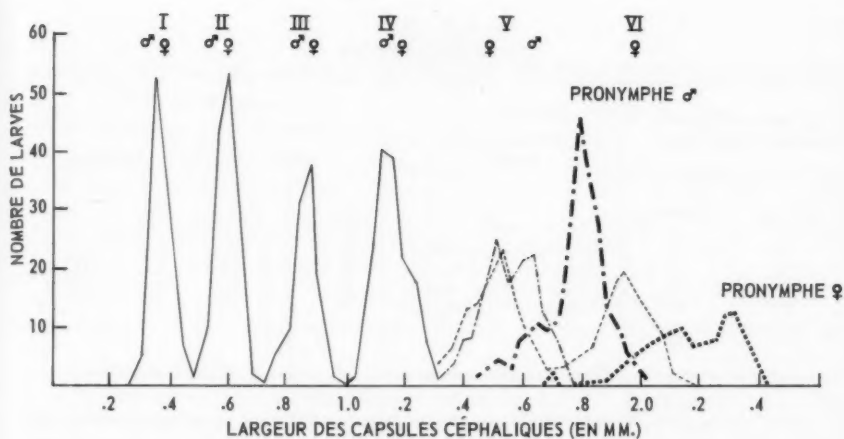
Fig. 7.   Largeur des capsules céphaliques.

Larve: L'élevage isolé de 30 larves en laboratoire a montré que celles du sexe mâle subissent cinq mues alors que celles du sexe femelle en ont une de plus. La dimension moyenne des capsules céphaliques des larves à divers âges a été établie grâce à la mesure de 1,200 individus récoltés au hasard dans le champ à des intervalles de 3 jours. Les mesures étaient prises au niveau des yeux à l'aide d'un oculaire micrométrique. A partir du 4e âge, il a été possible de séparer les sexes par dissection. Les résultats de nos mesures sont donnés graphiquement dans la Figure 7.

A part les dimensions de la tête et du corps, les divers âges larvaires se ressemblent beaucoup. Il existe toutefois quelques caractères que l'on peut utiliser pour les séparer, notamment le nombre de soies et, dans les descriptions qui suivent, nous utiliserons toujours le 3e segment abdominal pour décrire l'emplacement des soies à l'instar de Yuasa (1923).

A sa naissance la larve a une couleur foncière crème, avec les yeux, les mandibules et les griffes des pattes thoraciques de couleur brun rougeâtre, sans aucune tache ou dessin. Le 3e segment abdominal porte une quinzaine de soies d'inégale longueur montées sur des verrues. Après quelques heures d'exposition à la lumière la tête tourne au noir-brillant.

Au deuxième âge la larve a une tête noir-brillant, un corps de couleur foncière vert pâle ornementé d'une série de 12 taches minuscules de couleur noire portant chacune deux soies d'inégale longueur sur l'abdomen, juste au-dessus des stigmates. Le tergum du dernier segment abdominal est orné d'une tache noire bordée de quelques soies. Le 3e segment abdominal porte de 23 à 24 soies.

Les larves du troisième âge ont une tête noire garnie d'une bande jaune pâle courant le long des sutures frontales, les joues, le clypeus et à la base des mandibules. Les 12 taches de couleur noire au-dessus des stigmates sont plus grandes et une autre série de 10 taches également noires, mais beaucoup plus petites sont maintenant visibles sous les stigmates. Le 3e segment abdominal porte 35 ± 2 soies disposées sur les mêmes verrues qu'à l'âge précédent. La couleur générale de la larve varie du jaune pâle au vert pâle.

Au quatrième âge on remarque aucun changement de la couleur de la tête et du corps. Les deux séries de taches notées à l'âge précédent, de chaque côté

TABLEAU I

Longévité des adultes

Nombre d'insectes sous observation		Conditions de captivité	Longévité en jours			
			Mâles		Femelles	
Mâles	Femelles		Moy.	Ext.	Moy.	Ext.
5	5	Accouplés — au jeûne	2.7	2 - 5	3.8	2 - 5
11	11	Accouplés — alimentés	6.6	4 - 14	8.4	3 - 11
30	47	Vierges — au jeûne	2.2	2 - 6	3.3	2 - 6
20	17	Vierges — alimentés	8.2	5 - 16	8.3	3 - 15
66	80					

de l'abdomen, sont plus prononcées et des plages orangées sont maintenant visibles sur les côtés du prothorax et du 8e segment abdominal. Le nombre de soies sur le 3e segment abdominal s'élève maintenant à 47 ± 3.

Les larves des deux derniers âges, soit le quatrième et le cinquième, se différencient seulement par leurs dimensions. La plage orangée sur le prothorax s'est élargie pour couvrir le mésothorax. Le 3e segment abdominal porte maintenant 52 ± 3 soies. La coloration foncière du corps est vert pâle.

La pronymphe est facile à distinguer des âges précédents par les dimensions des taches dont le diamètre a triplé (Fig. 4). De plus, la pigmentation solide de la tête devient morcelée. La couleur verte du corps change au jaune orangé au moment où la larve cesse de manger. La longueur totale du corps varie de 16 à 22 mm.

Cocon — Les cocons sont formés de deux enveloppes; celle à l'intérieur est brun pâle, translucide et lisse, tandis que celle à l'extérieur, grossière, comprend des fils de soie auxquels sont agglutinés des débris végétaux ou des particules terreuses (Fig. 6). Dans les milieux humides, comme dans le bois pourri ou les feuilles mortes, on ne trouve que l'enveloppe interne. Le cocon a la forme d'un cylindre aux extrémités arrondies et mesure de 12 à 15 mm. de longueur sur 6 à 7 mm. de largeur.

Biologie et Cycle Evolutif Annuel

Peu après leur sortie du sol, les adultes se rendent en volant sur le feuillage des peupliers qu'ils explorent en tous sens, en s'arrêtant de temps en temps pour sucer les gouttelettes de sirop secretées par les glandes nectarifères situées à la base des feuilles. Leur activité s'accroît pendant les heures chaudes de la journée et on les voit alors voleter autour ou dans la cime. Cependant, leur vol est lourd et il est facile de les capturer à la main. Maintes fois, lorsqu'on vient pour les toucher, ils se laissent choir sur le sol et tombent en état d'immobilité réflexe pendant quelques secondes.

Dans nos études sur la ponte à l'extérieur, de 1956 à 1958, la longévité de 188 adultes des deux sexes sous observation a été en moyenne de 7 à 10 jours et de 2 à 3 semaines chez quelques individus. Les insectes en captivité au laboratoire ont vécu un peu moins longtemps. Les valeurs qui résument nos observations sur ce sujet (Tableau I) montrent que les femelles survivent de un à deux jours aux mâles et que la durée de vie des individus vierges et accouplés diffère peu. Toutefois, les sujets nourris d'eau sucrée vivent de deux à trois fois plus longtemps que ceux maintenus à jeun.

TABLEAU II
Fécondité des femelles

Année	Nombre de femelles pondeuses	Nombre d'œufs			
		Expulsés		Expulsés et dans les ovaires	
		Moy.	Max.	Moy.	Max.
1956	13	74.0	156	90.0	156
1957	74	49.7	113	66.7	191
1958	83	76.5	252	104.0	260

Au cours de nos élevages, le nombre de femelles a été sensiblement supérieur à celuis des mâles, soit un coefficient sexuel de 4 à 1. En Ontario, Raizenne (1954) en a observé un de 3 à 1 et Della Beffa (1949) en Italie, un autre se rapprochant de 2 à 1. Cette disproportion des sexes s'annule, d'une part, parce que chaque mâle peut féconder plusieurs femelles et que, d'autre part, les émanations des femelles attirent ceux-ci à de grandes distances. La parthénogenèse chez cette espèce est du type arrhénotoque.

Les femelles fécondées ou vierges peuvent pondre le jour même, si leur émergence se produit à bonne heure. La ponte retarde d'une journée pour celles écloses sur la fin de l'après-midi. Cependant, par temps froid et pluvieux, cette période se prolonge de plusieurs jours. Généralement, les femelles déposent la majorité de leur stock d'œufs au cours de leur seconde journée de vie, puis elles continuent à pondre quelques œufs chaque jour jusqu'à leur mort. Les pondeuses sont surtout actives pendant les journées chaudes et claires et demeurent pratiquement inactives lorsque la température se maintient au-dessous de 62°F., ou pendant les jours de pluie.

Un fort pourcentage des femelles meurent sans avoir réussi à pondre la totalité de leurs œufs. Afin de déterminer le nombre d'œufs total produit par individu, nous avons confiné des femelles accouplées dans des manchons de mousseline de 20 pouces de longueur et de 6 pouces de diamètre, englobant un rameau de peuplier dans notre champ d'expérience. Nous avons visité quotidiennement les manchons pour décompter et étiqueter les œufs déposés au cours de la journée précédente. A la fin de la période d'observation, nous avons examiné au microscope les gaines ovariques des femelles pour dénombrer les œufs non expulsés. Les résultats de ces observations, résumés au Tableau II, montrent que le nombre d'œufs produit par femelle varie de 66 à 104, mais seulement les trois-quarts environ sont expulsés.

Avant de pondre, la femelle explore la surface supérieure des feuilles, pour finalement enfourcher le pétiole à environ 5 à 10 mm. du limbe. Elle introduit graduellement sa scie sur un des côtés du pétiole, à angle droit, découpe une petite fente longitudinale dans laquelle l'œuf est déposé (Fig. 1). Tout ce processus se déroule en une minute environ. Ensuite, la femelle continue à pondre toute une série d'œufs régulièrement espacés, du même côté du pétiole, jusqu'à ce que sa tête touche à la branche. Rendue à ce point, elle se retourne sur le pétiole et recommence à pondre du côté opposé, au niveau du premier œuf pondu.

Il existe un rapport étroit entre le nombre d'œufs déposés sur chaque pétiole et la longueur de celui-ci. Bien entendu les espèces de peuplier à longs pétioles portent en moyenne le plus grand nombre d'œufs (Tableau III).

TABLEAU III
Nombre d'oeufs par pétiole

Essence	No. feuilles échantil- lonnées	Longueur moyenne du pétiole en mm.	No. oeufs moyen par pétiole	Distance moyenne entre les oeufs en mm.
P. nigra L.	123	31.9	12.3	1
P. tremuloides Michx.	96	35.4	15.4	—
P. alba L.	100	41.6	18.0	—
P. balsamifera L.	157	42.1	15.0	1.7
P. deltoides Marsh.	145	59.2	17.4	2.4
P. grandidentata Michx.	103	67.9	23.3	—

Oeuf — Au cours de son développement, l'œuf augmente considérablement de volume, comme cela a été observé chez une foule d'autres mouches-à-scie. Dans une série d'observations, nous avons enlevé 18 œufs de leurs logettes et nous les avons déposés sur un papier-filtre humidifié à l'intérieur d'une boîte de Petri. Les œufs fraîchement récoltés mesurent en moyenne 1.30 mm. de longueur sur .45 mm. de largeur et, peu avant leur éclosion, ils atteignent 1.46 mm. sur .68 mm., soit une augmentation de 14 pour cent en longueur et de 32 pour cent en largeur. En augmentant ainsi de volume les œufs exercent une pression sur les parois de leurs logettes qui finissent par s'écarter en déchirant l'épiderme supérieur et laissent voir une partie du chorion (Fig. 6).

Près de 5,000 œufs, étiquetés immédiatement après leur ponte et examinés par la suite tous les jours jusqu'à leur éclosion, ont servi à déterminer la durée du développement embryonnaire à l'extérieur. Le Tableau IV présente les résultats de ces observations, ainsi que les températures moyennes observées pendant les périodes correspondantes.

Larve — Dès leur naissance, les larves écloses des œufs pondus sur un même pétiole se rassemblent à la face inférieure de la feuille, près de la pointe. Pendant les trois premiers âges, elles se contentent de brouter l'épiderme inférieur; mais, à partir du quatrième âge, elles transpercent le limbe de part en part. Elles se tiennent toujours étroitement serrées avec la tête dirigée vers le bord de la blessure; c'est la position dite en "parallèle" (Fig. 1). Toute la ligne recule au fur et à mesure que la blessure s'aggrandit. De temps à autre, certains individus se retirent temporairement de la ligne, peut-être pour se reposer et rentrent quelques minutes plus tard, dans le rang en se frayant un chemin avec la tête.

TABLEAU IV
Durée du développement des oeufs

Nombre d'oeufs	Temp. moyenne au cours de la période en °F.	Durée en jours	
		Moyenne	Extrêmes
240	54	38	37 - 40
320	59	28	25 - 36
200	62	21	17 - 27
140	63	22	21 - 23
270	63.5	21	18 - 23
720	64.3	19	17 - 23
1500	64	19	18 - 23

TABLEAU V
Durée du développement larvaire en jours

19 mâles			18 femelles		
Age	Durée		Age	Durée	
	Moyenne	Extrêmes		Moyenne	Extrêmes
I	3.4	2 - 4	I	4.3	3 - 5
II	2.0	1 - 4	II	2.0	2 - 3
III	2.3	2 - 3	III	2.4	2 - 4
IV	2.3	1 - 3	IV	2.9	2 - 6
V	3.0	3 - 4	V	2.9	2 - 6
VI	3.5	3 - 4	VI	3.7	2 - 5
			VII	3.3	2 - 5
Total	16.5		Total	21.5	

En certaines circonstances, les larves d'une même colonie cessent soudaine-ment de manger, se retirent vers l'arrière et se disposent en forme d'étoile, toutes les têtes dirigées vers un même point du limbe et les corps légèrement arqués; c'est la formation dite en "rosette" (Fig. 3). D'autres fois encore, les larves d'une même colonie se dissocient pour former un peu en retrait de la bordure de la blessure, mais sans ordre bien défini, deux ou trois formations en parallèle.

Certains aspects de l'instinct grégaire des larves du *T. viminalis* ont été étudiés par Goidanich (1958) qui lui a donné le nom de "plésiotropisme". A ce stade de nos études, il nous est impossible d'expliquer ce phénomène. Cependant, l'observation du comportement de 25 colonies pendant toute une journée a montré que chaque colonie se déplace en moyenne sept fois pour adopter l'une ou l'autre formation et le passage de l'une à l'autre se fait avec ou sans transition. Parfois même une partie des larves sont en formation parallèle tandis que les autres se disposent en rosette.

Tous nos essais dans le but de provoquer artificiellement l'une ou l'autre de ces formations n'ont donné aucun résultat probant. Il reste cependant que l'in-stinct grégaire chez les larves de cette espèce est très puissant, car lorsqu'on disperse les larves d'une colonie sur un même rameau, elles se recherchent immé-diatement. Si bien que 15 à 18 heures plus tard, on les retrouve groupées géné-ralement en deux ou trois nouvelles colonies.

Cet instinct grégaire se conserve au moment des migrations. Lorsqu'une première feuille a été dévorée aux deux-tiers, la colonie émigre en bloc sur une autre feuille. Les larves se rendent d'habitude sur une feuille voisine en direction de l'extrémité du rameau, soulignant ainsi leur phototropisme positif. A partir de ce moment, les larves ingèrent une quantité énorme de nourriture et les migrations deviennent obligatoirement de plus en plus fréquentes. Au cours de son développement une colonie larvaire émigre de 6 à 9 fois et détruit le feuillage sur une longueur de 8 à 12 pouces. Cependant, lorsque les populations larvaires sont élevées le feuillage vient à manquer et les larves doivent parcourir de 5 à 10 pieds sur l'arbre avant de trouver leur nourriture.

Le nombre et la durée du développement de chacun des âges larvaires furent déterminés par l'observation directe de 19 larves mâles et de 18 larves femelles élevées individuellement en laboratoire. Les résultats de ces observations, résumés au Tableau V, indiquent qu'en moyenne chaque âge dure de 2 à 4 jours et que

TABLEAU VI

Quantité moyenne de feuillage dévoré à divers âges larvaires en cm.[2]

Ages larvaires	9 mâles	19 femelles
I	.23	.29
I	.39	.41
III	.78	1.05
IV	1.65	3.93
V	4.36	5.41
VI	5.44	8.15
VII	—	11.22
Total	12.85	30.46

le développement larvaire total s'effectue en 16.5 jours pour les mâles et en 21.5 jours pour les femelles.

Nous avons également déterminé en laboratoire la quantité de feuillage du peuplier de Lombardie consommé au cours de chaque âge et pendant toute la durée du développement larvaire d'un certain nombre d'individus des deux sexes. Nous avons mesuré au planimètre la surface de chaque feuille donnée en pâture aux larves avant et après chaque mue. D'après ces mesures (Tableau VI), la quantité de feuillage dévoré est surtout considérable au cours des derniers âges et la consommation globale est d'environ 31 cm.[2] chez les larves du sexe femelle et de seulement 13 cm.[2] chez elles du sexe mâle, qui ont un âge de moins. Or, comme la surface moyenne des feuilles du peuplier de Lombardie est d'environ 30 cm.[2], chaque larve consomme au cours de son existence l'équivalent de une demie à une feuille.

Pronymphe — Quelques jours après la dernière mue, les larves cessent de manger, leur coloration passe du vert au jaune orangé et après quelques heures de repos, elles descendent le long du tronc ou se laissent choir sur le sol. A ce moment les larves fuient la lumière directe du soleil et se réfugient en masses dans les endroits sombres. C'est là, de préférence, qu'elles forment leurs cocons. Les larves tissent leurs cocons dans les anfractuosités de l'écorce, les débris de toutes sortes qui jonchent le sol ou à peu de profondeur dans le sol.

Une faible partie des larves de la génération printanière poursuivent leur évolution et se transforment au cours de la même saison, tandis que celles provenant de la génération estivale demeurent toutes en diapause jusqu'au printemps suivant. Certaines pronymphes peuvent même rester en diapause pendant au moins deux ans; ceci avait d'ailleurs déjà été observé par Downes (1925) dans ses élevages conduits en Colombie-Britannique. Les larves de la génération printanière, qui poursuivent leur développement au cours de la même saison, se transforment en chrysalides au bout de 10 à 12 jours et les adultes apparaissent 6 à 10 jours plus tard.

A la latitude de Québec, il se produit deux générations par année, mais la seconde est toujours de faible amplitude et la majorité des larves ne parviennent pas à atteindre leur maturité avant l'arrivée des grands froids de l'automne. Par exception, en 1959, grâce à un climat exceptionnellement favorable, toutes les larves de la deuxième génération réussirent à compléter leur évolution et à filer leurs cocons vers la mi-septembre. Un examen des données météorologiques de la région de Québec, de 1948 à 1958, a révélé que des conditions semblables ont prévalu en 1953 seulement.

A la Figure 8, on trouvera les dates de l'apparition des divers stades de l'insecte au cours des années 1956, 1957 et 1958.

COCONS 1955

1956

ADULTES
OEUFS
LARVES
COCONS
ADULTES
OEUFS
LARVES
COCONS = NIL

COCONS 1956

1957

ADULTES
OEUFS
LARVES
COCONS
ADULTES
OEUFS
LARVES
COCONS = NIL

COCONS 1957

1958

ADULTES
OEUFS
LARVES
COCONS
GÉNÉRATION ESTIVALE = NIL

MAI   JUIN   JUILLET   AOUT   SEPTEMBRE
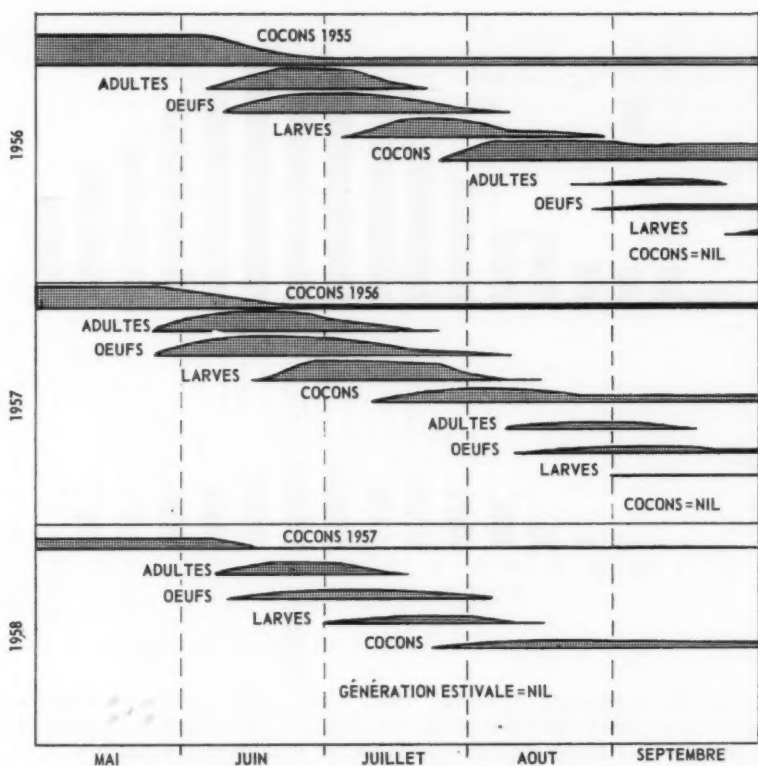
Fig. 8.   Cycle évolutif annuel.

Facteurs Naturels de Mortalité

Parasites

Malgré sa grande abondance, *T. viminalis* est peu parasité. Les auteurs qui ont étudié cet insecte ne mentionnent que trois espèces de parasites: *Ichneumon annulator* F., *Bessa harveyi* (Tnsd.) et une autre tachinaire non identifiée. Dans nos élevages, nous avons obtenu les espèces suivantes: une tachinaire, *Compsilura concinnata* Meig., un ichneumon, *Mesoleius* sp., une espèce non identifiée de la famille des Braconidae et une espèce de Pteromalidae du genre *Tritneptis*.

Il semble que les trois premières espèces qui s'attaquent aux larves aériennes peuvent difficilement tenir l'hôte en échec. Cependant, *Tritneptis* sp. qui parasite les pronymphes dans leur cocon dans une proportion de 4 pour cent sur le terrain, prolifère rapidement dans les stocks de cocons gardés en laboratoire. A la température du laboratoire, la durée du cycle évolutif complet de ce minuscule parasite a été très rapide, soit environ 3 semaines depuis la ponte jusqu'à l'éclosion des adultes. La brièveté de ce cycle explique la présence de ce parasite presque sans interruption sur le terrain durant tout l'été. Les femelles de ce parasite dans nos élevages ont pondu en moyenne 25 œufs chacune.

Prédateurs

Sans doute à cause de l'odeur nauséabonde que la larve inquiétée dégage, grâce à ses glandes odorifères placées sous l'abdomen, le nombre d'individus dé-
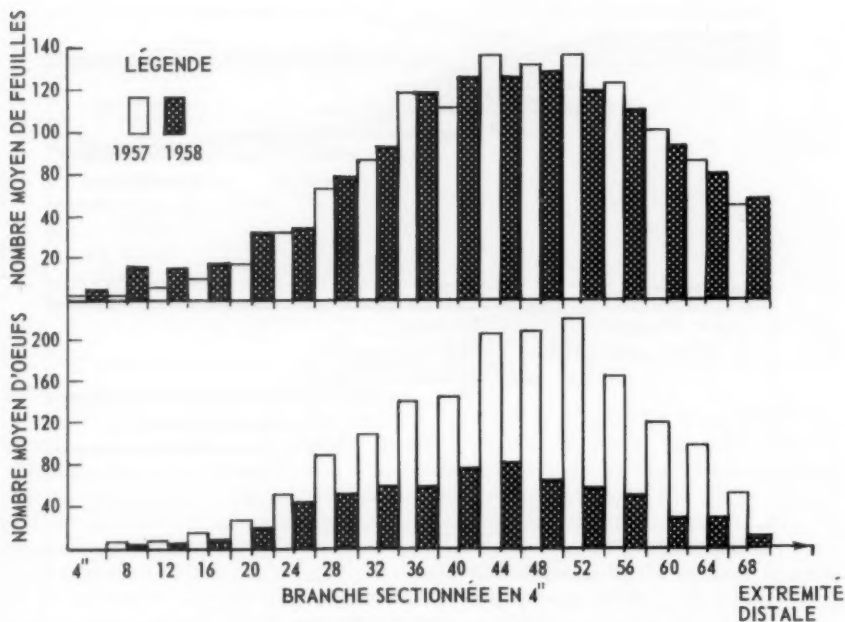
Fig. 9. Distribution du feuillage et des oeufs sur une branche.

truits par les prédateurs de toutes sortes n'est certainement pas considérable. Nous n'avons jamais observé d'oiseaux en train de s'en nourrir et Downes (1925) rapporte que les volailles refusaient les larves qu'il leur offrait à manger.

En une seule occasion, nous avons observé sur le terrain une grande quantité de cocons vidés selon toute apparence par un petit mammifère insectivore que nous n'avons pas réussi à capturer. En laboratoire, des souris à pattes blanches, *Peromyscus musculatus* (Weg.), se sont attaquées sans hésitation aux cocons du *T. viminalis*.

A l'occasion, nous avons également remarqué une araignée de la famille *Argyopidae* et une tenthrède du genre *Macrophyia* qui s'attaquaient à des larves âgées. Mais le prédateur le plus fréquent est un Pentatomide, *Apateticus cynicus* (Say), dont les nymphes dévorent les jeunes larves, et les adultes, les larves âgées.

Maladie

De tous les facteurs naturels de mortalité, le plus important est sans contredit une virose à polyhèdre. Cette maladie est apparue à Québec vers la fin de juillet, en 1957, et elle a détruit près de 80 pour cent de la population larvaire (Smirnoff et Béique, 1959). En 1958, la maladie, encore très virulente détruisit 90 pour cent des larves de la génération printanière et la population tomba à un niveau numérique extrêmement faible à partir de la génération suivante. La maladie couvrait alors un grand territoire, car nous avons récolté des larves malades dans un rayon de 25 milles autour de la ville de Québec.

Autres facteurs de mortalité

Le simple frottement des feuilles sur les rameaux les jours de grands vents peut entraîner la destruction d'un certain pourcentage des œufs et ceci se produit
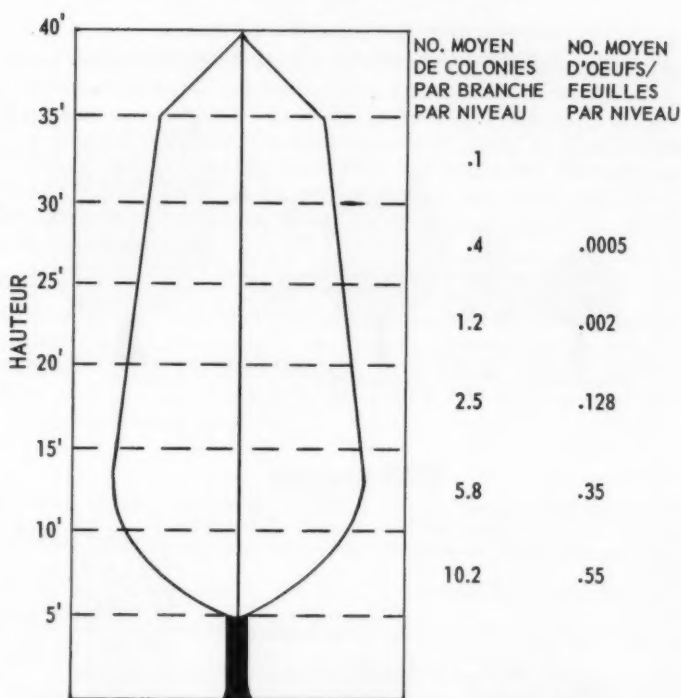
Fig. 10. Distribution de la population sur arbre entier.

plus fréquemment sur le tremble et le peuplier de Lombardie. Les pluies et les vents violents détruisent aussi une forte proportion des populations larvaires aux quatre premiers âges. Pour vérifier ce fait, en 1956 et 1957, nous avons étiqueté de nombreuses colonies, que nous avons ensuite rigoureusement comptées tous les jours. Au cours de violentes tempêtes de 30 à 40 pour cent des jeunes larves ont été projetées sur le sol.

Enfin, mentionnons que lors des déplacements massifs des pronymphes à la recherche d'un site favorable à la confection de leur cocon, un grand nombre d'entre-elles meurent en passant sur les pavés surchauffés par le soleil.

Ecologie

Lorsqu'on examine des arbres fortement défoliés par *T. viminalis* on remarque immédiatement que la population de l'insecte se concentre surtout sur les branches au bas de la cime. Ceci s'explique du fait que les femelles sont mauvais voiliers et se tiennent de préférence entre 5 et 10 pieds du sol et rarement plus haut que 25 pieds. De plus, les larves sont grégaires et se déplacent peu de l'endroit d'où elles sont nées.

Afin de confirmer les conclusions tirées de ces simples observations, nous avons cherché d'abord sur les rameaux l'endroit où les œufs sont déposés. Dans ce but, 172 branches d'environ 5 pieds de longueur ont été prélevées au hasard sur des peupliers de Lombardie dans le champ. Ces branches ont été ensuite sectionnées en tronçons de 4 pouces de longueur et toutes les feuilles et les œufs présents ont été soigneusement dénombrés. Les valeurs obtenues et présentées
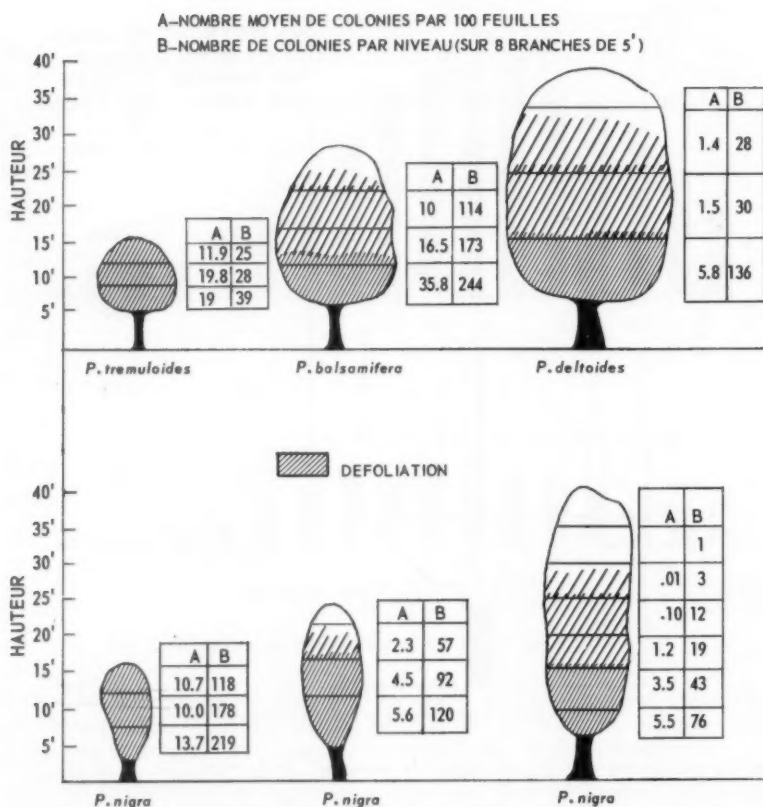
Fig. 11. Distribution de la population sur diverses espèces de peuplier.

schématiquement à la Figure 9 montrent que le nombre d'œufs est proportionnel à la quantité de feuillage présent.

En vue de déterminer à quel niveau dans la cime et dans quelle direction les œufs sont pondus de préférence, nous avons échantillonné quatre peupliers de Lombardie de 35 à 40 pieds de hauteur, en prélevant sur chacun d'eux et aux quatre coins cardinaux une branche complète à tous les 5 pieds d'intervalle dans la cime. Chaque branche fut ensuite examinée comme précédemment pour décompter le nombre de feuilles et d'œufs présents. Les résultats sont donnés schématiquement dans la Figure 10. En se référant à cette figure, on voit que le nombre d'œufs va en décroissant en fonction de la hauteur, si bien qu'à 25 pieds du sol on n'en trouve plus. Ceci explique que les arbres de plus de 25 pieds de hauteur n'ont que la partie inférieure de leur cime totalement défoliée. A la suite de cette constatation, on pouvait supposer à priori que, lors des attaques massives de l'insecte, les arbres de faible hauteur sont complètement dénudés, tandis que ceux de grande taille conservent un petit bouquet de feuillage au sommet de la cime. Ce fait a été vérifié par l'échantillonnage de diverses espèces de peuplier selon le mode décrit précédemment (Fig. 11).

Résumé

Au cours des cinq dernières années, la tenthrède du peuplier, *Trichiocampus viminalis* (Fall.) a causé des défoliations importantes dans le secteur de Québec, chez les peupliers ornementaux.   Le cycle évolutif de l'inspecte comprend deux générations, mais la deuxième est numériquement faible et généralement peu d'individus réussissent à compléter leur développement avant l'arrivée des froids de l'automne.   L'insecte est encore peu parasité et une virose qui, en certaines années détruit presque toutes les larves de la première éclosion, constitue le principal facteur de mortalité.

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(Reçu le 1 février, 1961)

The Biology and Behaviour of the European Pine Shoot Moth, *Rhyacionia buoliana* (Schiff.), in Southern Ontario I. Adult[1]

By P. J. Pointing

Forest Insect Laboratory, Sault Ste. Marie, Ontario

Introduction

The European pine shoot moth, *Rhyacionia buoliana* (Schiff.), has been recognized as a pest of pine plantations since it was described in 1776. Neugebauer (1952) stated that 32 susceptible pine species were known and that scarcely any species were rejected by the insect. Following its accidental introduction into North America about 50 years ago (Busck, 1914) the shoot moth became a serious pest of red pine, *Pinus resinosa* Ait., which appears to be the most susceptible species (Heikkenen and Miller, 1959). Watson (1947) described the shoot moth as "the most destructive insect affecting hard pines in southern Ontario, and the most difficult to control". Plantations have been damaged so severely that the planting of red pine has been virtually discontinued within the pest's range.

The general biology of the European pine shoot moth in the eastern United States has been described by Friend and West (1933), in England by Brooks and Brown (1936) and in Sweden by Butovitsch (1936). These authors have included comprehensive reviews of the earlier literature. Subsequent research in North America has been concerned primarily with the direct chemical control of the shoot moth and the assessment of insecticides (Friend and Plumb, 1938), (Stearns, 1953), (Connola *et al.*, 1954), (Haynes *et al.*, 1958), (Flink, 1959), (Butcher and Haynes 1958, 1959). Butcher and Haynes (1960) concluded that although a number of insecticides reduced shoot moth populations significantly, the method of application used in the tests would be impractical under forestry conditions. In Europe, preventive rather than control measures have been emphasized. Neugebauer (1949) maintained that direct control practices would have little or no lasting effect owing to the habits of the pest. Rather he stressed the influence of climate on outbreaks and cultural practices designed to increase the vigour of plantations and hence to reduce their susceptibility to shoot moth attack (Neugebauer, 1949, 1952) (Voûte, 1957).

Although the shoot moth was first recorded in Ontario in 1925 (McLaine, 1926), Hutchings (1926) believed that it had been present for 12 years or more. The insect spread from the shores of Lake Erie in a northeasterly direction (Fig. 1). Its northern limit, virtually unchanged over the past ten years, corresponds approximately to the minimum winter isotherm of $-20°F.$, which has been suggested as the limiting temperature (West, 1936; Rudolf, 1951; Batzer and Benjamin, 1954).

Except for a brief description of the early stages (de Gryse, 1932) and several reports concerning parasites (Coppell and Arthur, 1954; Watson and Arthur, 1959; Juillett, 1959, 1960a, 1960b), no detailed accounts of the biology of the shoot moth in Ontario, the northern limit of its range in North America, are available. In 1955, intensive studies designed to provide the knowledge fundamental to our understanding of this pest were initiated near Elmira, Ontario. This location was particularly advantageous in that it was situated near the centre of the "continuous" distribution of the shoot moth in Ontario (Fig. 1).
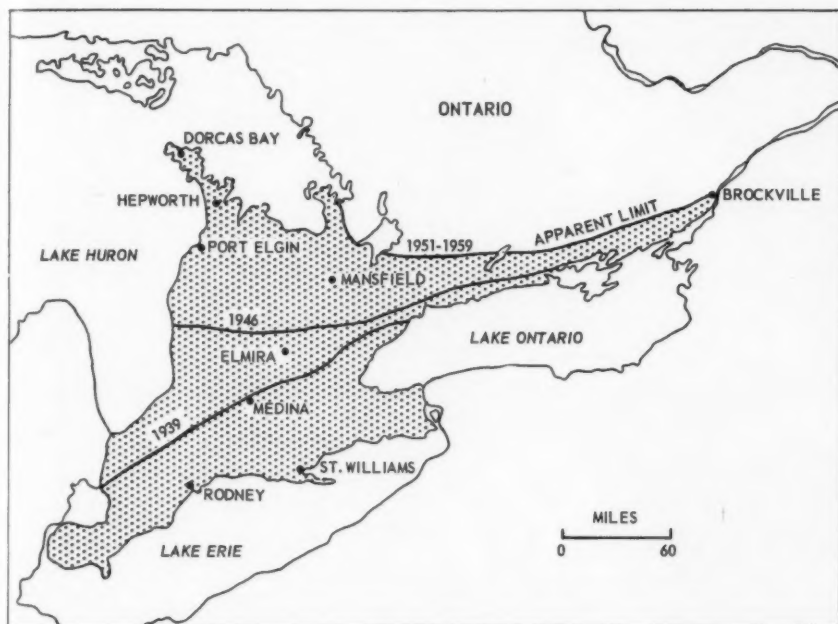
Fig. 1. The current "continuous" distribution of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.), in Ontario.

The tract comprises eight irregular blocks, ranging in size from five to 15 acres of dry, sandy, farm land which was abandoned about 20 years ago and subsequently planted between 1946 and 1950 with forest trees. Although some admixtures of red, Scots, white, and jack pine, as well as white spruce and European larch were originally planted, red pine predominates owing to the subsequent failure of the other species or to their relatively small proportion in the original planting. Here, a temporary field establishment was set up to serve as a base from which long and short-term studies could be conducted. Supplementary studies are currently being carried out in red pine plantations scattered from north to south over the range of the insect at Rodney, Medina, St. Williams, Mansfield, Port Elgin, Hepworth, and Dorcas Bay.

The present paper, the first of two describing the biology and behaviour of the shoot moth, is confined to the adult and based on studies at Elmira only, unless otherwise noted. The remaining stages will be included in the second.

Because the data on behaviour are presented in two papers, it is desirable to orient the reader by presenting the following brief account of the life history of the shoot moth in Ontario. Adults emerge from mid-June through mid-July and lay their eggs on pine shoots where they hatch in about two weeks. The first- and second-instar larvae feed on needle tissue enclosed within the needle sheath. The third instar larvae hollow and destroy from one to several buds during the late summer before passing the winter in or on a bud concealed under a mass of hardened pitch. As tree growth starts the following spring the larvae moult, then resume feeding in the developing shoots. Pupation occurs during late May or early June in chambers within hollowed shoots or buds.

TABLE I

The influence of spring weather on the seasonal emergence of the European
pine shoot moth, Elmira, Ontario.

Year	Typical weather	Emergence period	
		Start	End
1955	Hot, dry	5 June	1 July
1956	Cool, wet	26 June	27 July
1957	Moderate	16 June	10 July
1958	Moderate	16 June	16 July
1959	Moderate	17 June	16 July

Emergence

Just before pupation, the last instar larva cuts a circular hole in the wall of
the mined bud and then caps the opening with a mixture of silk and pitch. At
the end of the pupal period the pupa wriggles up the silk-lined chamber within
the bud, pushes slowly through the fragile, brittle covering of the exit and forces
itself through the opening until the abdomen jams in the hole (Fig. 2). Only
about one per cent of the pupae emerge completely from the chamber and drop
to the ground, although protruding pupae can be induced to wriggle free of the
exit opening by repeated disturbances. After about half an hour the pupal case
splits dorsally and the adult emerges, resting on or near the empty pupal case
while the wings are expanding. The moth, with wings fully-expanded, runs to
an exposed position at the top of the bud or adjacent needles, where it holds the
wings vertically until they are dry (Fig. 3), after which the moth retreats to the
needle bases or to the base of the bud until evening (Fig. 4).

The seasonal occurrence of adults was determined by the daily recording,
removal, and subsequent sexing of empty pupal skins from 30 entire trees and
over 500 individually-tagged, infested bud clusters. This study revealed that
adults are present from four to six weeks and that spring weather may advance or
retard the period considerably (Table I). During unusually hot, dry seasons,
when emergence occurs mainly in June, it coincides fairly closely with that in
Connecticut and New Jersey (Friend and West, 1933) and in Ohio (Miller and
Neiswander, 1955). During cool, wet seasons the period is later, mainly in July,
corresponding approximately to that in a number of European countries — France
(Vilmourin, 1917), England (Greenfield, 1914), Germany (Escherich, 1931) and
Sweden (Butovitsch, 1936). In general, however, the emergence period in
southern Ontario is one to two weeks later than that in the eastern and central
United States and from two to four weeks earlier than that in north-central
Europe. Figure 8 shows that cool, wet weather during the spring (1956) also
delays host tree development, so despite differences in the calendar dates, the
flight periods from year to year remain approximately synchronized with the
appropriate development of the host. The figure also shows that there is a

Figs. 2-7. Pupa and adults of *Rhyacionia buoliana*. 2. Pupa immediately before adult
emergence. 3. Adult drying wings. 4. Adult at rest during the day. 5. Receptive female on
needle-tip during the evening. 6. Mating pair. 7. Female adult attempting to oviposit on a
needle.
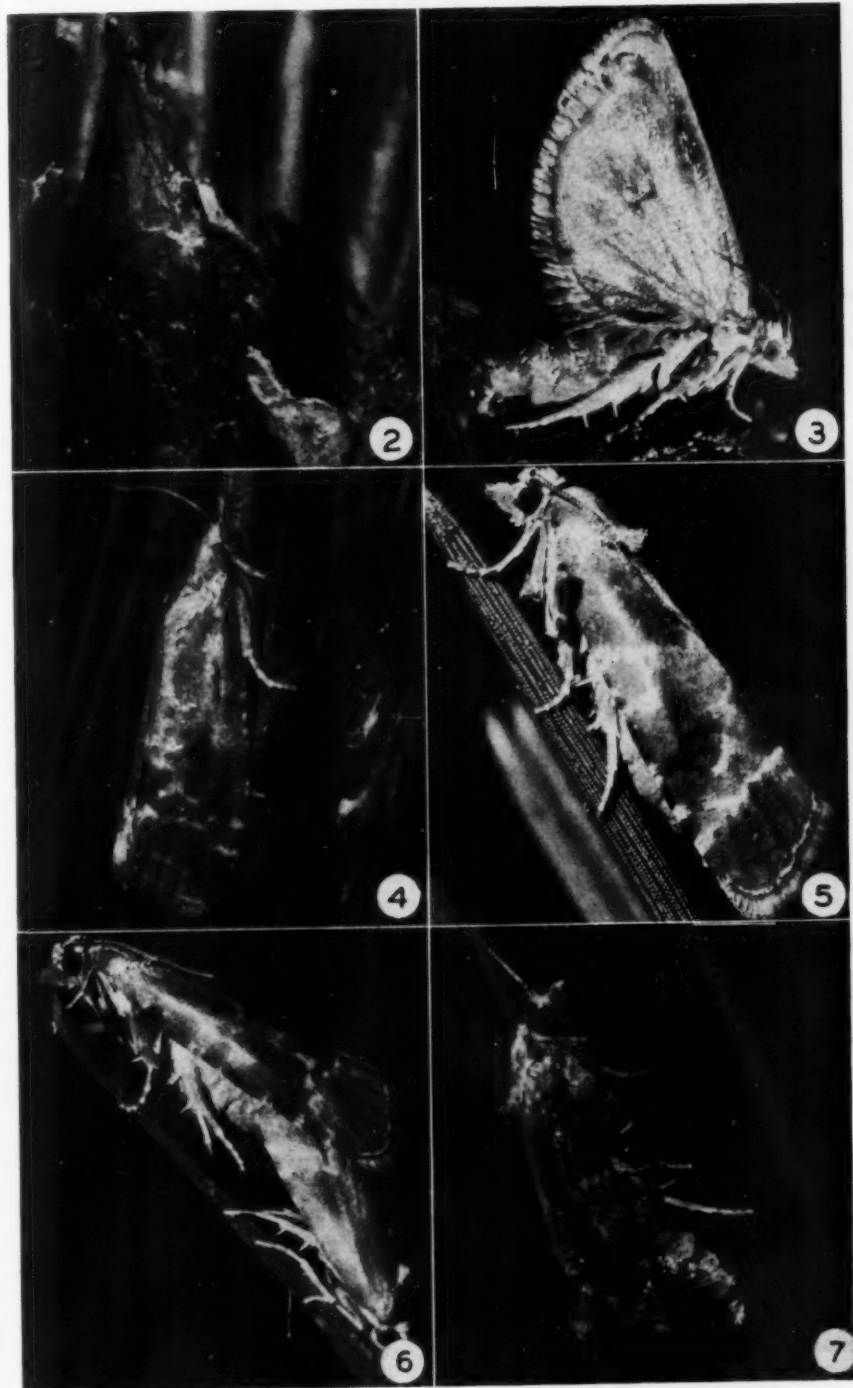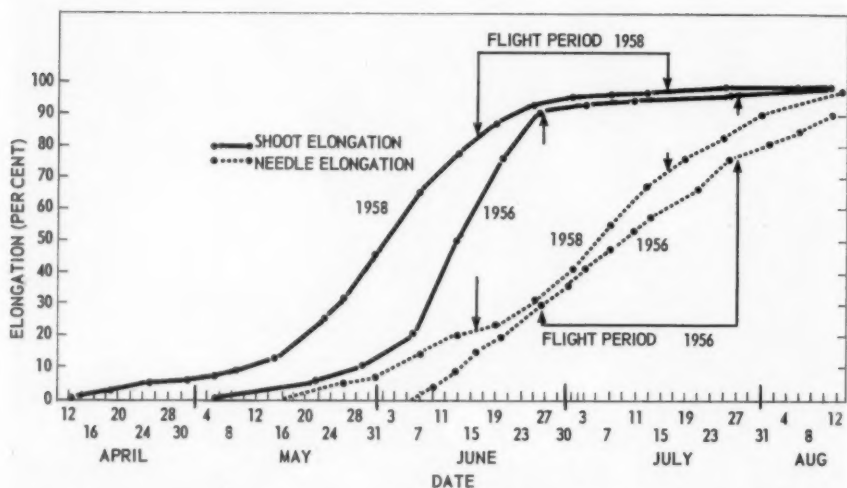
Fig. 8. Occurrence of the flight period of the European pine shoot moth and of the seasonal growth of red pine shoots (based on mean values for 20 tagged shoots) during a typical spring, 1958, and an unusually cool, wet spring, 1956. Elmira, Ontario.

tendency for phenological differences to diminish as the summer progresses although they may persist throughout the entire growth period.

Emergence is protandrous. Figure 9 shows that male emergence, in the field, is typically from three to five days ahead of that of females. Similar results have been obtained in the insectary (Friend and West, 1933; Miller and Neiswander, 1955). Emergence in the insectary at the field establishment was somewhat delayed and prolonged over that in the field.
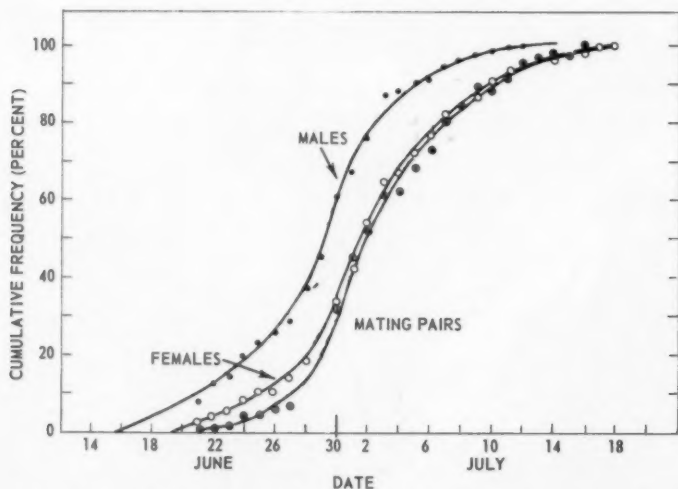
Fig. 9. The seasonal distribution of emergence and mating of the European pine shoot moth in 1958 based on 313 ♀♀ and 147 ♂♂, the total emergence from 30 entire trees. Elmira, Ontario.
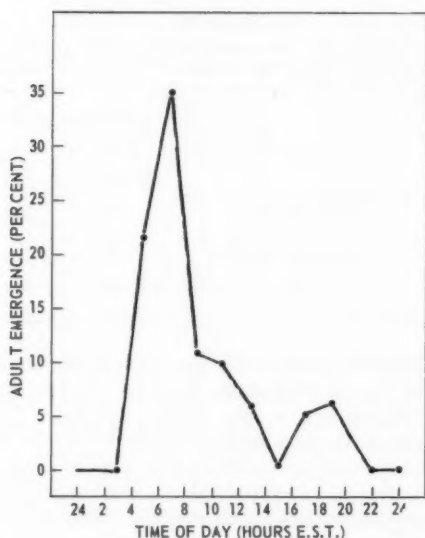
Fig. 10. The daily emergence pattern of the European pine shoot moth under field conditions based on emergence from 480 infested bud clusters. Elmira, Ontario.

A diurnal emergence pattern was revealed. To facilitate the actual observation of emergence, 480 infested bud clusters were forced on to the points of closely-spaced nails that were driven vertically upward through narrow boards. These, in turn, were fixed on posts in the plantation at a height convenient for the observer. To expedite inspections, clusters lacking obvious, unopened pupal exits were discarded. Every 10 minutes the shoots were inspected to observe the emergence and behaviour of the adults during peak periods. Figure 10 shows a prominent peak in emergence between 0600 and 0700 hr. E.S.T. An apparent peak during late afternoon and early evening requires additional data to firmly establish its reality. In contrast, over half of the 591 moths emerging from buds stored in emergence boxes appeared in the collecting vials during the afternoon. Presumably, then, the statement that emergence usually takes place during the afternoon (Brooks and Brown, 1936) refers to insectary emergence. The lack of physical cues such as abrupt increases in temperature or light within the boxes may destroy the circadian rhythm or perhaps the moths emerge in the morning and remain quiescent for some time in the boxes before entering the vials.

Adults emerge with little difficulty from pupal cases fixed in buds. The dissection of 387 tagged, infested bud clusters, collected after emergence was complete, showed that 302 adults, or 78 per cent, had emerged. The 913 adults collected from emergence boxes represented 81 per cent of the original pupae and pupal skins. Pupae removed from the buds fared poorly, however, 7 of 109 males and 63 of 131 females emerged, a mean of only 29 per cent. Apparently the semi-rigid fixing of the pupal case in the bud facilitates the escape of the adult and may also reduce loss from desiccation.

Sex ratios differed significantly from 0.5, the value obtained for the shoot moth by Friend and West (1933) and by Miller and Neiswander (1955). During a three-year period the mean sex ratio was 0.72 ♀ ♀ for a total of 5,019 adults reared in emergence boxes. A ratio of 0.69 was obtained for 988 moths that had emerged from tagged bud clusters on trees.

TABLE II

Sex ratio of the European pine shoot moth based on adults reared from
samples collected from 1954 through 1956, in various localities.

Collection period	Insect state	Number of adults		Sex Ratio
		Female	Total	
Early spring	Instars IV - V	791	1,774	0.45
Late spring	Instars VI-pupae	1,782	2,661	0.67
Early summer	Pupae	1,441	2,067	0.70

Several factors apparently affect the sex ratio of the shoot moth. Table II, for example, indicates that a progressive increase in the relative abundance of females may occur during the spring feeding period. The severity of the infestation may also affect the proportion of females (Table III). The relatively greater mortality of males may result from competition with female larvae, their inability to cope with physical or biotic factors, such as evaporation or resin flow, and from genetic changes associated with the age of the infestation.

Pre-mating Flight and Mating

Throughout the heat of the day moths are so easily disturbed by an observer, or by foraging ants, reduviids, nabids, and other predators that they frequently dart from the trees into adjacent or lower branches of the same or nearby trees, or drop to the ground. In the evening moths are less readily disturbed and their behaviour can be observed more closely. The first spontaneous activity occurs at about 1700 hr. as the moths gradually emerge from their seclusion at the needle bases and move toward exposed positions near the needle tips (Fig. 4-5). Moths start flying at sunset on clear days, or somewhat earlier if the day is overcast or if the trees are shaded. The adults are easily distinguished from other moths by their size and flight pattern. The flying moths are primarily males searching for mates, although an occasional female may be seen. Meanwhile virgin females remain quietly at the tips of the needles.

When approaching a receptive female the male beats its wings rapidly and curls the tip of its abdomen upward, opening and closing the claspers.

TABLE III

Sex ratio of the European pine shoot moth in collections from plantations
differing in severity of infestation.

		Infestation		
		Light	Severe	Total
Emergence	Males	446	1647	2093
	Females	641	2827	3468
	Total	1087	4474	5561
	Sex Ratio	0.59	0.63	

$$X^2 \quad 6.88, \text{ d.f.} = 1, \text{ P} = 0.01$$
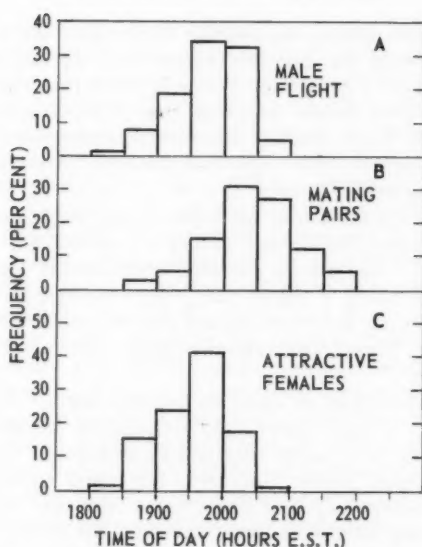
Fig. 11.   The daily distribution of: (A) the male pre-mating flight based on 160 5-minute counts; (B) the formation of mating pairs (based on 294 pairs); (C) the virgin females attractive to males based on 125 female-days.   Elmira, Ontario.

Occasionally, the female, when contacted by the male, makes abortive attempts to escape.   After the union has been completed the pair becomes quiescent, the female directed outward along the needle, the male inward (Fig. 6).   Coition may start early in the evening at the beginning of the flight period, breaking up after 2100 hr. or thereabouts, and by 0100 hr. over half of the pairs have usually separated, although some may remain joined until sunrise if the night is cool. When a pair separates, the male moves a few inches from the female then slowly retires to the needle bases.   The position of the female remains unchanged for some time, frequently until daybreak, when it, too, seeks the shelter of the needle bases usually on the same shoot.   During the following day she may occasionally shift her position slightly on the bud or twig, thus avoiding direct sunlight.

The daily flight period of males was established by recording the number of flights per five-minute interval between two rows of trees six feet apart over a 30-foot length of row, an area of approximately 0.004 acres.   To provide a daily and seasonal record of mating, the number of pairs and their location were recorded hourly or half-hourly during the period of adult activity on a group of 30 trees which included those inspected daily for emergence and which surrounded the area where flight counts were made.

Figure 11A shows that the peak of flight intensity occurred between 1930 and 2030 hr. and that flight decreased rapidly thereafter approaching zero at 2130 hr.   Moths were rarely seen flying later in the evening although they occasionally flew through the beam of a flashlight, or were stimulated to fly if the beam were focussed on them.   These observations are in contrast to those of Benjamin *et al.* (1959), who state that moths generally fly after dark.

Figure 9 shows that the seasonal occurrences of female emergence and of mating pairs are virtually coincident.   The strong correlation between the numbers of females emerging during the day and the number of mating pairs

located on the same tree during the evening of the same day (r = 0.94) suggests that females usually mate the day they emerge and do not move from the tree until they have mated. Figure 11A and 11B show that the daily peak in the formation of mating pairs occurs later than that of flight intensity and that some pairs are formed after flight ceases. The latter phenomenon may have resulted from males crawling on trees after flight had ceased, or possibly from the inclusion of pairs missed during earlier counts.

Wind influences the behaviour of males during the mating period. During the evening a single virgin female may attract a large number of males to the tree where she is resting. On windy evenings unsuccessful males disperse almost immediately after the union is made. On calm evenings, however, unsuccessful males may continue flying and crawling around trees for several minutes after the pairing takes place. These observations suggest that a scent released by the females attracts males.

This apparent attraction of males to females during the flight period was investigated further. Virgin, mated, and ovipositing females were confined in small cylindrical cages, two inches long and two inches in diameter, constructed of nylon net and acrylic plastic (lucite). Ten cages containing females were suspended from a 20-foot length of fine copper wire that was stretched parallel to the rows at tree-top height, or were hung on the trees, to determine under what conditions females attract males. As a measure of attractiveness, the number of males present within one foot from a cage was recorded at 10 minute intervals. Males were attracted and tended to congregate around the trees closest to the cages suspended from the wire and downwind from them. Shifting the "attractive cages" along the wire quickly dispersed the groups, which reassembled near the cages in their new locations. Consequently, each cage was removed from the wire and placed on a separate tree where more uniform results were obtained when the effect of the variable distances from cage to tree were eliminated. The following synopsis shows that only virgin females attracted males.

Status of female	Attractive	Not Attractive
Virgin-fresh	31	2
Virgin-ovipositing	7	3
Mated	0	6

Eleven virgin females were observed for eight consecutive evenings. The peak numbers of males were attracted to a female the third evening after she emerged. Individual females remained attractive for just over one hour per evening but remained attractive for from two to seven days. This prolonged attractive period increases the chances of mating should males be prevented from flying for several days by adverse conditions. Figure 11C shows that the daily periods of attractiveness correspond closely to those of male flight intensity and suggests that either the scent released by females stimulates males to fly or that similar levels of physical factors stimulate females to release the scent and males to fly.

Oviposition and Fecundity

In the field individual, naturally-occurring females, or those radioactively tagged with Co[60] by the method used by Green *et al.*, (1957) were located on trees early in the evening before the flight period, and their behaviour was recorded until darkness prohibited further observations. Numbered paper tags were used to follow the flight paths from tree to tree, and insect pins bearing small paper markers identified the twigs and needles where oviposition had been attempted. The latter were subsequently collected and the number of eggs recorded.

During the evening of the day after mating, a mated female crawls to a needle tip and beats her wings rapidly and may make short flights or flop back among the needles. Occasionally an attempted oviposition precedes the first short flight, which coincides with the onset of male flight. After landing, the female crawls rapidly headfirst down a needle to the vicinity of the needle sheath where she reverses her position and backs down to the needle base. Exploratory motions are made with the extended ovipositor and if it contacts a flat surface one or two eggs are deposited. Females typically lay single eggs, rarely more than two or three in one spot, but females incapable of flying may deposit eggs in clusters. Eggs are laid on any flat surface, which may be needle bases, bark, bud scales or needles (Fig. 7). If it is unsuccessful in reaching a flat surface, the female usually crawls through the foliage toward the tip of the shoot until a suitable site is reached. Immediately after ovipositing, the moth scrambles rapidly to a needle tip and almost invariably beats her wings or flies before attempting further oviposition. Short flights that become progressively longer later in the evening, and on successive evenings, generally precede oviposition attempts. These flights are less erratic than those of males, possibly because the females being heavier and having relatively shorter wings are incapable of manoeuvring rapidly. Since the positions of radioactively tagged females usually remained unchanged overnight it may be assumed that few fly spontaneously after dark.

On approaching trees, females often dart haphazardly into the foliage, apparently making little attempt to select an oviposition site. Of the 96 eggs found at tagged sites 72, or 75 per cent, were on current shoots. This distribution reflects the relative abundance of current shoots, which are from two to five times as abundant as year-old shoots, and does not necessarily imply selection by the moths. There was no evidence to support the hypothesis that females selected "the green, tender bark of new growth" (Brooks and Brown, 1936). Oviposition occasionally occurs on grass blades on which moths may alight by choice or by accident.

To investigate oviposition in the insectary, mating pairs were collected in the field during the evening and confined in empty, inflated cellophane bags. Females readily deposited eggs on the transparent walls of the bags and counts were made at two-hour intervals from 0800 until 2200 hr. Figure 12 shows that the oviposition period may last three weeks and that a peak is reached on or about the third day after mating. High temperatures advance the peak and shorten the period (Fig. 13A), whereas low temperatures delay the peak and prolong the period (Fig. 13B). The two-hourly counts indicated that the daily peak rate of eggs laid per hour per individual, as well as the peak in numbers of moths participating, occurred between 1800 and 2000 hr. and that two-thirds of all the eggs were deposited between 1600 and 2000 hr. This period corresponds with that established by field observations on free-flying moths.

Table IV indicates that the fecundity of females confined in cellophane bags varied little from year to year, although the mean of 116 eggs is considerably lower than the mean of 168 reported by Miller and Neiswander (1955). Estimates of the number of eggs laid per female in the field were obtained by restricting individual mating pairs to cages on selected trees. An average of 63 eggs per female for 13 mated pairs was counted when the trees were dismantled and inspected critically. A shorter adult life occasioned by predators in the cages, or increases in other activities, e.g. flying, which would reduce the energy available for egg laying may have caused this apparent reduction in fecundity.
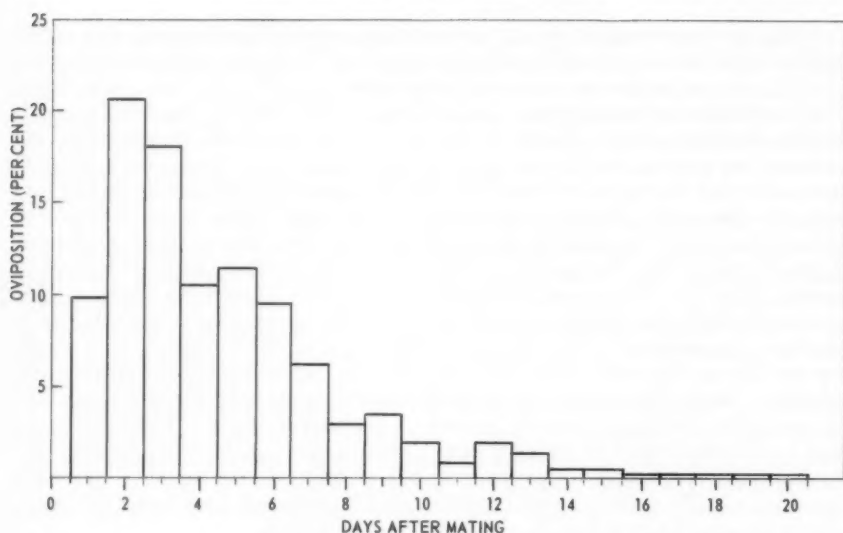
Fig. 12. Daily mean oviposition after mating of the European pine shoot moth in an insectary based on 54 females. Elmira, Ontario.

The excess of females, particularly toward the end of the emergence period, suggests that late-emerging females may either not mate or mate only with males that have already mated several times. Accordingly the male members of mating pairs collected in the field were caged and permitted to mate up to four additional times with virgin females. Table V shows that males are capable of mating, with at least partial success, four times and perhaps more often, since they could have mated several times before they were captured. The apparent increase in sterility in successive matings is probably of little consequence since sterile eggs were rarely seen in the field.

Longevity and Predation

Females confined in cellophane bags stored in a hot, unshaded tent lived an average of 11 days whereas those kept in a well-ventilated, shaded insectary lived 23 days. In a screened cage measuring 12 by 12 by 6 feet and enclosing four trees in the plantation, the mean life span of 11 radioactively tagged females was 8.8 days. Fourteen, free-flying, tagged females lived an average of only 5.4 days, although a tag *per se* does not reduce the longevity of shoot moth adults (Green

TABLE IV

The fecundity of the European pine shoot moth confined in inflated cellophane bags.

Year	Number of females	Number of eggs	Eggs per female
1955	14	1,527	109
1956	27	3,131	116
1957	32	3,808	119
1958	22	2,812	128
1959	17	1,929	113
1960	37	4,045	109
Totals	149	17,253	115.7
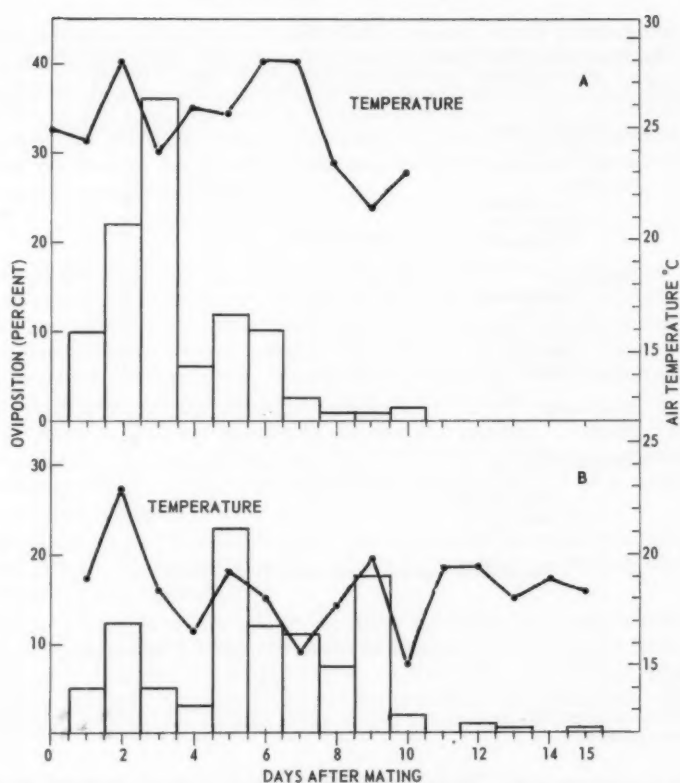
Fig. 13. The influence of temperature on the oviposition of the European pine shoot moth in an insectary; (A) high temperature (9 females, 1003 eggs); and (B) low temperature (6 females, 731 eggs).

et al., 1957). The marked reduction in the adult life of free-flying individuals may have resulted from their increased activity stimulated by disturbance from predators.

To a large extent the ultimate fate of shoot moths attacked by predators will be determined by the strength and agility of the moth relative to that of the predators. No vigorous adults were observed being captured and held by ants on the trees; however, flightless or feeble individuals were often caught, par-

TABLE V
The results of multiple matings of male shoot moths with virgin females.

Number of matings	Frequency	Females producing viable eggs	Per cent viability
1	36	31	73
2	17	10	72
3	5	2	66
4	1	1	46

TABLE VI

Radioactively contaminated arthropods etc., recovered following the release of adult female European pine shoot moths tagged with Co[60].

Contaminated predator	Number recovered
Arachnida	
Linyphiidae	4
Salticidae	4
*Phalangida	3
Insecta	
Formicidae	9
Nabidae	6
Reduviidae	4
Carabidae	2
Other	2
Bird faeces	7
	41
Dead moths	11
Total recovery	52
Total release	188

Predation — based on recovery $\dfrac{41 \times 100}{52} = 79\%$

based on release $\dfrac{41 \times 100}{188} = 22\%$

* Probably a scavenger.

ticularly on the ground. Many reduviids and nabids were observed feeding on moths but no captures were witnessed. A recently-emerged but flightless shoot moth escaped twice from a reduviid before the latter gave up the attack which lasted more than half an hour. Nabids that attack in a like fashion must experience similar failures. Spiders inhabiting red pine also prey on the moths. Small shoot moth adults were commonly trapped on platform webs (Linyphiidae) whereas larger moths tore free and flew off. Similarly, many moths escaped from the small orb webs (Argiopidae). However, jumping spiders (Salticidae) successfully captured large, active female moths. Ground beetles associated with shoot moth remains presumably captured living moths or found them dead on the ground. Thus despite the abundance of predacious species associated with shoot moth on red pine relatively few are capable of capturing large, vigorous individuals.

Ants, reduviids and nabids "patrolling" foliage often passed within a centimetre or so of motionless shoot moths, apparently unaware of their presence. Infrequent, chance contacts caused the moths to fly or to drop to the ground. Moths thus disturbed during the day were commonly caught on the wing by asilids, or by ants and carabids on the ground. Consequently, the "patrolling" of twigs by some predators may indirectly influence predation inasmuch as the disturbed moths may become easy prey for other predacious species.

The recovery of radioactively contaminated predators, scavengers, bird droppings, dead moths etc., provided additional information. Table VI shows that ants and ants' nests were most frequently contaminated. The predation

based on predators and moths recovered in the area of search (four chains square) was almost 80 per cent; based on the total number of moths released it was approximately 20 per cent. Nevertheless, the data indicate that a fairly large proportion of the adult shoot moth population was eliminated by predators. In fact, it is likely that most moths eventually fall prey to some predator, but if predation on females occurs at or near the end of oviposition there will be no effect on the population trend.

Summary

The adults of *Rhyacionia buoliana* (Schiff.) started emerging when red pine shoots and needles had completed 85 and 25 per cent respectively of their growth. This correspondence was maintained from year to year despite differences in calendar dates of three weeks or more. Cumulative emergence of males preceded that of females by several days. Emergence success *in situ* on trees was approximately 80 per cent and provided a sex ratio of 0.7 females.

Emergence occurred primarily in early morning. Adults remained quiescent unless disturbed during the daylight hours; spontaneous activities, such as pre-mating flight, mating and oviposition, were confined to a short period before and after sunset.

Receptive, virgin females advertised their positions by releasing a scent which attracted males. The latter were guided more effectively to the former in light winds than in calm conditions.

Maximum longevity and fecundity were exhibited by females confined in inflated, cellophane bags. The reduction in longevity and possibly fecundity of females confined outdoors in large cages or of free-flying individuals tagged with Co⁶⁰ could be attributed in part to higher temperatures and predation. The most common radioactively contaminated predators were ants and spiders.

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(Received June 9, 1961)

Ecology of Two *Prosimulium* Species (Diptera) with Reference to their Ovarian Cycles

By L. Davies*

Entomology Research Institute, Research Branch, Canada Department of Agriculture
Ottawa, Ontario

Prosimulium fuscum Syme and Davies, *P. mixtum* S. and D. and *P. fontanum* S. and D. form a complex of closely-related and largely sympatric species formerly known in North America (Twinn, 1936; Stone and Jamnback, 1955) under the single name *P. hirtipes* Fries, a well known species in the northern Palaearctic. The first step in demonstrating the multiple nature of the forms grouped under this name in North America was taken by Rothfels (1956) who showed by study of the larval salivary gland chromosomes that at least three non-interbreeding forms were present in eastern Canada. L. Davies (1957a) concluded from a study of specimens of all life-stages that none of the North American forms agreed with European *P. hirtipes*. A further step in the process was afforded by the work of Syme and D. M. Davies (1958), which erected the three species named above as a result of anatomical study of cytologically defined material, and showed that adult females of *P. fuscum* and *P. mixtum* could be reliably separated, mainly by features of the genitalia. The present work may be considered as a further step in the study of the common *Prosimulium* of eastern North America, by providing information on their ecology, thus amplifying the cytological and anatomical conclusions arrived at in the papers cited above.

Together with *Simulium venustum* Say, *P. fuscum* and *P. mixtum* comprise the great bulk of the black flies assembling at and biting man in an area near Ottawa, typical of the less elevated southern edges of the Laurentian Shield country of Quebec and Ontario; at higher elevation in the Shield, such as at Mont Tremblant and Laurentide Park, P.Q., the third member of the group, *P. fontanum* tends to replace the two latter species (L. Davies, unpublished observations). Ecological study of *P. fuscum* and *P. mixtum* therefore is an essential part of elucidating the facts behind the black fly problem in these areas.

In recent years Rubtzov (1955, 1956, 1958) has put forward a comprehensive theory regarding the need for blood for ovarian development in black flies. In Rubtzov's view, most species, apart from those incapable of biting through atrophy of their mouth parts, are "facultative blood suckers", in that the need for a blood meal to complete the first ovarian cycle depends on the level of nutrition of the larval stages. Where a stream affords adequate food matter, females with considerable food reserves are produced and these mature the first egg batch autogenously, while larvae in streams poor in food matter produce females with inadequate reserves and so must obtain a blood meal for completion of the first ovarian cycle. A fundamental point in Rubtzov's thesis is that the one and the same species exists as autogenous and anautogenous individuals, the nature of each in this regard depending on the food available in the larval habitat. This theory, if substantiated, would contribute greatly to understanding the ecology of black flies and the nature of the biting problem, and would explain many puzzling features of black fly attacks in many parts of the world. Particular attention was therefore given in the present work to studying the number of ovarian cycles undergone in the field by these species and the degree of dependence of these cycles on blood meals. This was done partly by direct observation in the field, partly by maintaining adults of known history alive in the laboratory to observe ovarian development, and partly by dissection of catches of females

*Present address:—Zoology Dept., University of Durham, England.
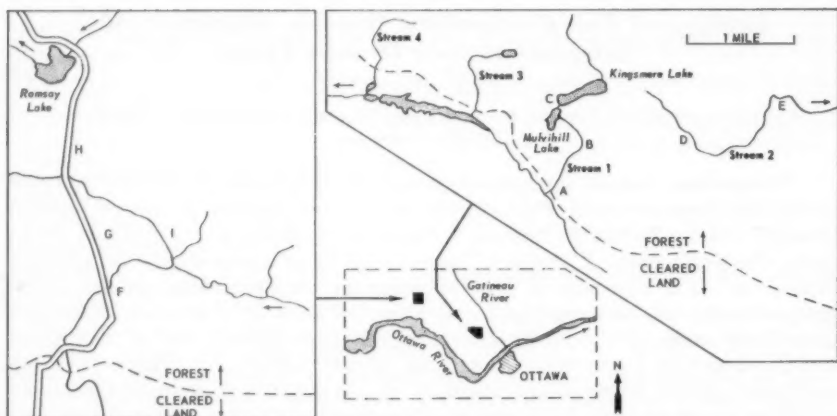
Fig. 1. Sketch map of the study areas, showing the streams sampled for *Prosimulium* larvae, and sites A-H at which samples of adults attracted to man were obtained.

attracted to man in the field throughout the season to determine the composition of the biting population at a particular time in terms of nulliparous and parous individuals. From this latter type of information various deductions can be made regarding the occurrence of autogeny in each species, particularly by comparing the timing and abundance of parous individuals with that of nullipars in each of the three seasons (1958-60) covered. The reproducibility or otherwise of field events can thus be taken into account in interpreting the facts particularly since, if Rubtzov's views are correct, larval food and hence the occurrence of autogeny would be expected to vary between different seasons and from place to place.

A further incentive to study the ovarian cycles of black flies resides in their known role as vectors of parasites (Lewis, 1953; Anderson, 1956; Bennett, 1960; Bennett and Fallis, 1960) knowledge of which is rapidly expanding in Canada, so as to suggest that these almost ubiquitous insects are probably involved as vectors wherever biting Simuliidae are represented. The occurrence of autogeny would be expected to modify this picture considerably, by affecting the efficiency of transmission even to the extent of determining whether a given species would or would not act as a vector in nature.

The Study Area

The salient features of the study area, situated 10-20 miles north west of Ottawa are shown in Fig. 1. The line separating the forested area from that cleared of trees coincides with the edge of typical Shield country, consisting of low hills rising about 500 feet above the almost flat cleared area. The forested hills have generally thin soil cover and the streams are rock-bottomed in the steep stretches which alternate with gentler reaches with gravel substratum. These small streams, one to three yards wide, are fairly typical of much of the *Prosimulium*-producing brooks of the hill areas of eastern North America, which in this case flowed through secondary hardwood forest consisting mainly of *Acer* and *Fraxinus*, with some *Fagus*, *Quercus* and other genera, as well as scattered conifers, mainly old trees. The canopy height is mainly at 20-30 feet and tree growth is sufficiently dense to produce relatively calm conditions near the ground on most days, so that the size of the adult *Prosimulium* catch was not markedly affected by wind. The points marked A-H (Fig. 1) are the sites at which frequent samples of black flies were collected by attraction to man.

TABLE I

Percentages of certain larval classes in samples of mixed *P. fuscum* and *P. mixtum* from streams in Gatineau Park, near Ottawa, 1957-58

	1.0 - 1.9 mm body length				Over 6.0 mm body length				Larvae with black histoblasts			
	Stream No.				Stream No.				Stream No.			
	1	2	3	4	1	2	3	4	1	2	3	4
Nov. 6	1.2	7.2	—	5.4	0	0	—	0				
19	0.6	4.7	5.5	14.8	2.0	0	0	0				
Dec. 5	1.1	—	8.2	4.6	1.6	—	4.9	1.8				
24	2.2	18.3*	0.7	13.4	11.0	3.3*	8.5	4.1				
Jan. 24	2.4	—	0	0.4	14.3	—	11.8	18.8				
Feb. 5	0.8	5.5	—	—	22.2	0	—	—				
21	0	—	0	—	35.3	—	18.2	—				
Mar. 10	0	0	0	0	61.8	27.5	27.4	16.5	0	0	0	0
24	0	—	0	0	51.0	—	47.1	26.2	0	—	0	0.1
April 8	0	—	0	0	71.0	—	81.3	53.0	17.5	—	11.1	0
15	0	—	—	—	70.3	—	—	—	28.0	—	—	—
21	0	1.0	—	—	77.5	23.2	—	—	43.1	11.7	—	—
28	0	—	—	0	80.4	—	—	74.0	61.5	—	—	30.2

*Dec. 16 sample.

Larval Development in Relation to Adult Seasonal Span

O'Kane (1926) and others showed that the present species hatch from eggs in autumn and early winter, reach the final instar in late winter and pupate and emerge in early spring. Samples of 100-1000 larvae were collected at fixed points at intervals from November, 1957 to April, 1958 from six streams in and near the study area, by lifting stones, twigs and leaves and removing all individuals visible to the naked eye. The body length of alcohol-preserved larvae thus obtained was measured while holding each specimen straight against a scale marked in 0.5-mm. units, a method sufficiently accurate for the present purpose where counting of 1-mm. size groups was required. Cytological examination of mature larvae from the streams sampled showed that in most cases mixed populations of *P. fuscum* and *P. mixtum* were being studied (Rothfels, personal communication). The samples did not contain first instar larvae although these were recovered by other methods.

The smallest larvae (1.0-1.9 mm. long) in hand collected samples correspond approximately to the second instar as shown by comparison of details of the submental teeth and of the number of main rays in the head-fans, both features showing change from one instar to the next. Since there is evidence (L. Davies, 1960) that the first larval instar is of only about two days duration, the occurrence of 1.0-1.9-mm. larvae in a sample can be taken to indicate that egg hatching has occurred within a few days prior to the sample date. Larvae known without doubt to be in the last instar by the presence of black pupal-filament histoblasts always exceeded 6.0 mm. body length in these samples. As an approximation larvae exceeding this length were taken to represent the last instar component of each sample.

Table I shows the proportion of each sample that consisted of 1.0-1.9 mm. and over 6.0 mm. body length, together with the percentage of the whole sample that had black pupal-filament histoblasts. Two important features are apparent; firstly, second-instar larvae occurred from early November until early February, showing that egg hatching extended over a period of at least three months. First

instar larvae were recovered from these streams in the following autumn as early as October 15, showing that egg hatching may extend over five months. Secondly, larval growth was proceeding throughout the winter, so that larvae accumulated in the last instar, which formed an increasing proportion of successive samples.   Stream temperature readings were made at the time each sample was taken, using an accurate mercury thermometer graduated at 0.2°F.   These readings are summarized as mean water temperatures with the number of readings in parentheses:—November, 43.9° (8); December 33.8° (7); January, 33.1° (3); February, 32.7° (13); March 10-11, 33.4° (16); March 24, 36.4° (5); April 8, 36.5° (4).   They show that from late December to early March water temperatures were below 34°F.   Since streams 1, 3 and 4 had during the whole of this period a complete 6-12 inch ice cover, overlain by one to five feet of snow, conditions were ideal for the maintenance of virtually constant water temperatures and it is unlikely that diurnal fluctuations exceeded 2°F. during late December-early March.   From the figures in Table I it follows that larval development from the second to last instar must therefore have been proceeding satisfactorily at 33-34°F. so that the lower threshold for growth in *P. fuscum* and *P. mixtum* larvae cannot be higher than this.   These species probably in common with many other *Prosimulium* with a similar annual cycle, seem well adapted to the cold conditions of the streams during most of the larval season, so that it is unlikely that development ever ceases owing to low temperatures.

The accumulation of larvae in the class exceeding 6.0 mm. body length during the winter (Table I) suggests that the temperature threshold for pupation is higher than 33-34°F.   In fact the first pupa was taken on April 8, when water temperature readings were around 36°F. during the daytime.   After this date the start of ice break-up led to conditions where diurnal fluctuations in water temperatures of larger amplitudes could take place, such as on April 15 when in stream 1 it varied at one place from 41.0° at 9.40 a.m. to 46.9° at 1.40 p.m., so that 'spot' temperature readings become of little value in determining the conditions to which larvae were subjected over periods of several days.

Despite the scatter of egg hatching over a period of up to five months, the accumulation of larvae in the last instar during the winter leads to considerable synchronization of adult emergence, the latter feature being abundantly confirmed by the adult studies given later (page 1118).   This synchronization would appear to be achieved by the higher temperature threshold for pupation as compared to that for larval development, a situation that appears to be basically similar to that worked out in detail by Corbet, 1958) for the pre-imaginal development of dragon flies.   Clear evidence of this process is discernible in a previous study of *Prosimulium* larvae by D. M. Davies and Syme (1958) where in their Fig. 1 the main change in sample characteristics was the reduction during the winter of the extreme range of larval dimensions so that large larvae were present as early as November, while March and April samples consisted of only slightly larger larvae but with none of the small larvae that existed alongside large specimens until February, showing that last instar larvae accumulated during the sampling period.

The proportion of larvae over 6.0 mm. body length just at the start of mass-pupation in mid- and late April (Table I) shows that, although considerable synchronization of emergence was achieved as described above, there were differences between streams in emergence pattern.   In streams 1 and 4 on April 28, 80 and 74 per cent respectively of each sample consisted of full-grown larvae, showing that emergence would be concentrated over a short period, a feature confirmed by frequent pupal collections (last pupae on May 9 and 10 respectively).   In stream 2 on April 21, only 23 per cent of the sample consisted of

TABLE II

Percentages of 1.0 mm size classes in two late winter
Prosimulium larval samples from three streams

Stream No.	1		4		2	
Class, mm	March 10	April 21	March 10	April 21	March 10	April 21
1.0 - 1.9	0	0	0	0	0	1.0
2.0 - 2.9	1.1	0	2.1	1.6	7.7	3.0
3.0 - 3.9	3.1	1.5	17.8	6.6	17.1	10.7
4.0 - 4.9	12.0	2.5	38.5	7.5	24.8	27.8
5.0 - 5.9	21.5	17.9	25.2	38.3	22.1	34.3
over 6.0	61.8	77.5	16.5	43.3	27.5	23.2
sample size	191	196	1041	240	181	393

mature larvae, showing that adult emergence here would be later and more
protracted, particularly so since 1.0-1.9 mm. larvae still existed.   The last pupae in
this stream were collected on May 25 but they almost certainly existed later than
this.   These differences were closely related to larval development in March and
April.   In stream 1 over 60 per cent of the March 10 sample were full grown, so
this class of larvae inevitably increased rather slowly to 80 per cent on April 28
and in effect the population was "marking time" for much of this period.   In
stream 4 only 16 per cent were full grown on March 10, but they increased
rapidly after this date.   The proportion of full grown larvae in stream 2 on the
other hand was low on both March 10 and April 21.

More detailed comparison of the situation in these streams in late winter is
afforded in Table II, showing the proportions of all size groups on two dates.
The main change between March 10 and April 21 in stream 1 was a reduction
in the size of the "tail" of immature larvae.   In the same period this process
occurred in stream 4, but the 2.0-2.9 mm. group were still present on April 21.
If the early larval stages, the second and probably the third instars in this case,
were of shorter duration than the 42-day period March 10-April 21, the 2.0-
2.9 mm. larvae still existing in stream 4 on April 21 must have hatched from eggs
after March 10.   The relatively short duration of these early stages is demon-
strated by the following figures, giving the percentages of each larval class in two
samples from stream 1, separated in time by only 18 days:—

larval class (mm.):—	2.0-2.9	3.0-3.9	4.0-4.9	5.0-5.9	over 6.0
Feb. 21	9.0	11.8	14.0	29.8	35.3
March 10	1.1	3.1	12.0	21.5	61.8

The changes show that in the three lowest size classes, most larvae had apparently
at least advanced to the next category within 18 days, and if eggs had been hatch-
ing during this period as they probably did, the real duration of the stages would
be even less.   In the period March 10-April 21 therefore, when stream tempera-
tures were higher, the duration of the smaller classes must have been far less than
the 42 day interval between these dates.   In stream 2 (Table II) the proportion
of full grown larvae was no greater on April 21 than it was on March 10
(actually the proportion was lower in the April 21 sample but this decrease is
small enough to have been a result of sampling error), and on the latter date
1.0-1.9 mm. larvae were present.   Since this class would be rapidly depleted by
growth, particularly in April when the stream was rapidly warming and ice-free,
even a small proportion of 1.0-1.9 mm. larvae could indicate extensive egg hatch-
ing.

TABLE III

Dates of first and last appearance of *Prosimulium* females at man near Ottawa

		1958	1959	1960	Mean span (days)
P. fuscum	First female	May 6	May 7	May 5	
	Last female	June 3	May 26	May 27	24
P. mixtum (nullipars only)	First female	May 6	May 8	May 6	28
	Last female	June 4	May 29	June 8	

To summarize, the differences between streams in the proportion of immature larvae on April 21 when pupation was well underway, largely reflect differences in the importance of egg hatching in late winter from stream to stream. Since larvae hatched from eggs before about mid winter accumulated in the last instar, presumably because temperatures were too low for pupation, it is the occurrence and extent of March-April egg-hatching that determines the duration and scatter of adult emergence. In the present case stream 1 would have an early and relatively short period of adult *Prosimulium* production, and stream 2 a long period and thus a later mid-point of the emergence curve. This characteristic of stream 2 in the spring of 1958 was further confirmed by finding in it half to full grown *P. mixtum* larvae on May 21, a time when other streams had been devoid of larvae for almost three weeks as far as could be determined by frequent searching. Occasional larval samples from stream 2 in the spring of 1959 and 1960 showed that this stream had a long period of adult production in these years also, so that the 1958 situation was not exceptional.

The relatively short period during which adults were produced from pupae in the study area is shown by the dates of first and last capture of females attracted to man (Table III). (Although scattered females would occur outside these dates, they probably constituted less than 5 per cent of the total population in these years). In *P. fuscum* the dates refer to parous females for reasons given later (page 1125), while the *P. mixtum* dates are for nulliparous females only, since their occurrence would be expected to agree more closely with the timing of emergence than would corresponding information for parous flies, which would have been on the wing for a longer period between emergence and capture. The average adult appearance period of 24 days in *P. fuscum* and 28 days in *P. mixtum*, may be compared with the prolonged egg hatching period of at least 5 months, and reflects the considerable synchronization of adult appearance effected by the features of larval development outlined above.

D. M. Davies and Syme (1958) found that although the limits of adult emergence in the two species largely coincided, the mid-point of *P. fuscum* emergence occurred sooner than that of *P. mixtum* in streams where the species co-existed. In the present work, in stream 2 where the species occurred in approximately equal numbers, the first sets of black-histoblast larvae collected always produced a preponderance of *P. fuscum* as identified cytologically, while later collections usually produced higher proportions of *P. mixtum*, in agreement with the findings of D. M. Davies and Syme. Since it was found impracticable to separate full grown larvae using submental teeth characters, counts were made of the number of main rays in the cephalic fan using cytologically defined material from all streams in the study area.

The results may be summarized as follows:—

	P. mixtum	P. fuscum
Range of fan ray number—	25-36	35-49
No. of full grown larvae determined—	142	156
No. of larvae in the zone of overlap, i.e. with 35 or 36 fan rays—	2	2

This shows that full-grown larvae of the two species can be separated by fan ray number, except for the small number involved in the overlap at 35 and 36 fan rays. For present purposes mature larvae in samples, with 35 or fewer rays were ascribed to *P. mixtum*, those with 36 or more to *P. fuscum*. (It should be emphasized that this method does not always seem to be practicable, because aberrant fan-ray counts were encountered in cytologically identified material from certain distant localities e.g. New York State and Western Ontario.)

A series of four samples from stream 1 were taken in 1958, that on April 8 being early and that on April 28 being late in the *Prosimulium* pupation season for this stream. The percentage of the total sample that consisted of black pupal histoblast larvae of the two species, identified by fan ray count was as follows:—

	P. fuscum	P. mixtum
April 8	0.7	16.8
” 15	1.9	26.1
” 21	4.0	39.1
” 28	2.5	59.0

Although stream 1 had a low proportion of *P. fuscum*, the above figures show that the mid-point for black histoblast larvae probably fell within the period April 15-21 for *P. fuscum* and within April 21-28 for *P. mixtum*, so that under identical conditions in this stream the former species on average would emerge as adults slightly sooner than the latter.

Female Abundance and Population Structure

Methods. Samples of females attracted to man were obtained at sites A—E shown in Fig. 1 on as many days as possible during the fly season. The collectors stood and intermittently moved within an area about 50 feet in diameter at each site, which were chosen so as to be sheltered from direct wind. Flies were netted as they arrived with a light, fine mesh net about 18 inches diameter. With practice it was possible to net virtually all flies very soon after arrival by making use of the fact that *Prosimulium* adults hover about the observer's head before attempting to land. Very few bites were sustained in the course of many hours work, and it was noticeable that if the observer ceased waving the net about his person, bites were sustained. In order to minimize the effects of variations between men in their attractiveness to *Prosimulium* and in their efficiency with the net, different collectors went to each site on different days. A sample of at least 50 flies per site per day was aimed at, and this usually took one to three hours collecting, periods of six to eight hours being spent when flies were scarce. The catch was placed in vials, labelled and placed in an ice jar, and frozen for storage in the laboratory at 10-15°F. until required.

Flies were dissected individually on a slide under a dissecting microscope in a drop of 0.7 per cent saline containing a trace of detergent (Lewis, 1953), and examined at a magnification of 50 to 120 X. The fly was placed on its right side with the head towards the dissector and the abdomen opened by a lateral longitudinal needle tear from about the third to eighth segment. The ovaries were gently squeezed and drawn out as intact as possible, and the ovarioles teased

apart and spread for examination. For special purposes the ovarioles were not teased apart, and instead the delicate outer ovarian membrane was gently pierced and groups of intact ovarioles manipulated with fine tungsten needles in order to preserve the details of the ovariolar intima and its contents, so that the follicle relics could be seen (Detinova, 1949; Lewis, 1960), transferring the slide for this purpose to a compound microscope and viewing with and without phase contrast.

In addition to determining the presence or absence of follicle relics, the existence of parasites was noted as well as the stage of development of the lowest follicle in each ovariole. These follicles were classified according to the system long used for mosquitoes, and modified slightly for use in black flies by Wanson and Lebied (1948). The presence and number of relict ripe eggs from previous gonotrophic cycles was recorded, as well as the amount of fat body. The main purpose of the dissections was to determine the proportions of nulliparous and parous flies present in each day's catch and in special cases to detect whether the parous flies had undergone more than one gonotrophic cycle.

Abundance

The number of flies caught as described above at a given place will vary from day to day through the influence of at least three sets of factors, namely:— (1) Weather conditions affecting the level of fly activity. (2) The size of the population present in an area of unknown size around the collector. (3) The proportion of this population consisting of hungry females seeking blood meals. The latter factor will in part be a complex function of the previous history of the fly population. To reduce the importance of the weather effect on catch size, geometric means of the number of flies taken per man per hour were calculated for five-day periods, and these geometric means are termed the "apparent abundance" in the following account. Periods of five days were chosen partly because major changes in the age composition of the population seemed to require about this length of time.

P. mixtum. Table IV, a, shows the apparent abundance of females at various sites in different years. As a basis for comparison, if one considers that the season is ended when the abundance falls below 10 flies/man/hr. it will be seen that the season lasted about 20-30 days. The 1958 figures form an extreme case in that the season lasted longer, with 20 flies/man/hr. in the sixth period, and the peak number fell in the fourth period instead of the third period as in 1959 at the same site. In *P. mixtum* the peak of apparent abundance was always associated with the appearance of parous flies and the evidence for this and a discussion of why it should be so is given later (page 1123). In 1958 at site E therefore, the long season and late peak seem to reflect a delay in the completion of the first ovarian cycle in this species, and a likely explanation of this is to be found in the remarkably cool weather of the first two five-day periods in that year, each period having a mean daily maximum of only 55° and 56°F. respectively. These readings are from the Experimental Farm, Ottawa, 10 miles from the study area and in open country. Maximum temperatures in the forested study-area are likely to have been even lower. In the third and fourth five-day periods the corresponding temperatures were 74° and 62°, and the sudden warming of the weather coincided with the appearance of parous flies and thus with increased apparent abundance. In 1959 the second five-day period was cool the mean daily maximum being 54°F., but this followed a very warm first five-day period (mean maximum 71°F.), which would hasten the processes involved in the ageing of the *Prosimulium* population from one entirely nulliparous to one composed

TABLE IV

Five-day geometric means of the numbers of *Prosimulium* females taken
by hand net per man per hour at sites in Gatineau Park

Site and year —	E 1958	E 1959	A 1959	A 1960	B 1960	C 1960	D 1960
5-day period No.			(a) *P. mixtum*				
1*	22	29	19	37	37	—	—
2	21	25	26	36	141	155	519
3	50	59	78	40	95	258	737
4	207	21	12	22	12	51	89
5	59	13	6	2	4	4	18
6	20	6	3	3	1	6	9
7	2	1	0	2	1	1	1
8	1	0	—	—	—	—	—
			(b) *P. fuscum*				
1*	67	13	9	20	48	—	—
2	15	7	11	8	61	72	75
3	50	12	14	8	33	27	8
4	35	2	2	3	2	29	2
5	5	0	1	0	1	1	0
6	1	0	0	0	0	0	0

*First 5-day period started on May 6, 1958; May 8, 1959 and May 9, 1960.

largely of parous flies. In agreement with this parous *P. mixtum* individuals appeared sooner in 1959 (see below).

Comparison of 1958 with 1959 figures for site E (Table IV, a) shows that there was a great decrease in apparent abundance of *P. mixtum* from the one year to the next, and site A in 1959 gave very similar low numbers. Comparing the corresponding figures for *P. fuscum* (Table IV, b) shows similar relationships, so that in both species there is good evidence for a real decline from 1958 to 1959, since weather differences through their effects on activity are unlikely to differentially affect each season as a whole.

In 1960 there were remarkable differences in apparent abundance of *P. mixtum* females between sites A-D (Table IV, a) involving an approximately tenfold increase from site A to D, with B and C intermediate, the differences being fairly consistent. The figures show that two- to four-fold differences in apparent abundance occurred between places separated by only 0.5-1.0 miles (e.g. A to B is 0.5 miles), and differences of up to 10X between sites A and D, separated by approximately 2.5 miles (see Fig. 1). Sites B-D were all close to stream sections observed to contain very large numbers of *Prosimulium* larvae in late April, while the section adjacent to site A had rather sparse larvae. The simplest explanation of the differences in apparent abundance of *P. mixtum* females between A-D in 1960 is that they reflected differences in the number of flies produced from the adjacent stream in each case. This cannot be directly substantiated because it is virtually impossible to sample the larval populations quantitatively, particularly in streams of this type. If the above explanation was largely correct, the figures in Table IV imply a rather feeble dispersal of flies from the stream of origin. If dispersal was vigorous it would cause disappearance of local concentrations of flies caused by highly local variations in fly production. The suggestion of relatively restricted flight range of *P. mixtum* females agrees with evidence on other *Prosimulium* species obtained in this work. At 1.5 miles west of site A, on the cleared plain, a stream producing large numbers of *P. multidentatum* Twinn was occasionally visited at the appropriate time, yet at site A not a single specimen of this species was taken.

TABLE V

Per cent of parous flies in total catch in *P. mixtum*

Site and year —	E 1958	E 1959	A 1959	A 1960	B 1960	C 1960	D 1960
May 6-8	0	0	0	0	—	—	—
9	—	—	0	3	0	—	—
10	—	—	—	2	22	—	—
11	—	8	0	7	—	—	—
12	0	14	31	—	—	—	—
13	10	23	64	39	72	—	—
14-15	0	30	—	—	—	—	—
16	4	—	—	84	92	37	90
17	—	36	76	86	86	86	78
18	—	37	65	—	—	—	—
19	—	82	96	92	88	87	94
20-21	93	89	84	81	97	95	—
23-24	—	—	95	92	—	91	—
25	—	89	87	88	100	88	99
26	98	85	90	82	—	—	—
27	95	—	83	84	92	90	99
28	95	—	91	—	—	—	—
29	93	—	99	—	80	—	—
30-31	—	—	—	100	100	100	98
June 1-2	100	—	100	—	100	100	96
3-4	97	—	100	—	100	100	100
5-6	100	100	100	100	—	89	50
8-18	100	—	—	80	100	—	100

Since site A was the only one situated at the edge of the forested area (Fig. 1), and since it produced the lowest apparent abundance figures the difference between sites A-D in 1960 could reflect movement of flies from the forest edge into its interior. However, the 1959 figure for site A (edge of forest) and E (about two miles from edge of forest) show very similar abundance levels, indicating no consistent movement of flies from the edge, and suggesting that the differences between sites in 1960 were probably a result of highly local variations in fly production.

P. fuscum. Apparent abundance figures (Table IV, b) show that, as with *P. mixtum*, there was a marked decline in numbers at site E from 1958 to 1959, and equally low figures at sites A and E in the latter year. Comparison of sites A-D in 1960 for *P. fuscum* shows interesting similarities and differences from the corresponding figures for *P. mixtum*. In both species site A gave the lowest figure but site D, at which *P. mixtum* was more than ten times as abundant as at A, produced a relatively high figure for *P. fuscum* in the second five-day period only, although it may have been equalled in the first period during which unfortunately this site was not worked. The main difference between the species in 1960 was that changes in apparent abundance between sites A-D were far smaller in *P. fuscum*, the extremes of variation in peak numbers being only 20 to 75 flies/man/hr., as compared with 40 to over 700 in *P. mixtum*.

Population Structure

Follicle relics indicating a previous gonotrophic cycle were large in both species and were similar in general features to those described and illustrated by Lewis (1960) for certain African *Simulium* species. Certain details however occurred in a manner not recorded by Lewis. The contents of the dilation of the ovariolar tunica were usually quite colourless, grey and granular. Where coloured matter occurred, as it did in a minority of specimens, it was red or

TABLE VI

Five-day geometric means of nulliparous (left column in each series) and parous (right column) *Prosimulium* females/man/hr.

Site and year —	E 1958		E 1959		A 1959		A 1960		B 1960		C 1960		D 1960	
5-day period No.						(a) *P. mixtum*								
1	22	0	25	4	17	2	33	4	28	9	—	—	—	—
2	20	1	17	8	11	15	6	30	15	126	55	100	62	457
3	43	7	13	46	12	66	5	35	8	87	7	251	46	691
4	12	195	3	18	3	9	3	19	1	11	7	44	2	87
5	4	55	3	10	2	4	0	2	1	3	0	4	2	16
6	2	18	0	6	0	3	0	3	0	1	1	5	3	6
7	0	2	0	1	0	0	1	1	0	1	0	1	0	1
8	0	1	0	0	—	—	—	—	—	—	—	—	—	—
						(b) *P. fuscum*								
1	8	59	2	11	2	7	2	18	3	45	—	—	—	—
2	1	14	0	7	0	11	1	7	1	60	3	69	3	72
3	2	48	1	11	1	13	0	8	0	33	0	27	0	8
4	0	36	0	2	0	2	0	3	0	2	2	27	0	2
5	0	5	0	0	0	1	0	0	0	1	0	1	0	0
6	0	1	0	0	0	0	0	0	0	0	0	0	0	0

brown in colour, and was confined to one or more small masses buried within the bulk of follicle debris, and often existed only in ovarioles towards one end of each ovary. Owing to the large size of follicular relics in *Prosimulium* no difficulty was encountered in separating parous from nulliparous flies.

P. mixtum. Table V shows the proportion of parous flies during the complete season at each site where the bulk of the catch was dissected, and shows certain constant features in each season. For the first few days the catch consisted entirely of nulliparous flies or a very low proportion (less than 10 per cent) of parous individuals. This phase was followed by a rapid increase in the proportion parous until about May 16-20 when it reached levels of over 70 per cent, and for the remainder of the season it fluctuated between 80 and 100 per cent. For purposes of discussion the adult *P. mixtum* season may thus be divided into three successive phases; first, that when nullipars predominated; second, that when the proportion parous was rapidly increasing, and third, that when the population attracted consisted virtually entirely of parous flies. Table V shows that the third phase was the longest, lasting at least as long as the other two combined, although it should be noted that after about May 23 in each season the population was in decline and after June 1 extremely low.

Geometric means of the number of flies/man/hr., corresponding to those for the total catch (Table IV, a) but this time for nulliparous and parous flies separately are given in Table VI,a. The unique situation in 1958 (site E) involving a delay in the peak of apparent abundance mentioned earlier (page 1120) is shown to reflect a delay until the fourth five-day period in the appearance of parous flies in any numbers, and reasons were given for believing that this was correlated with the consistently cool weather during the first two five-day periods in that year. At all sites in 1959 and 1960 when the weather was warmer at the corresponding times, parous flies appeared in numbers usually in the second or third five-day period.

In all complete series of geometric means except one (Table VI,a) parous *P. mixtum* females reached peak apparent abundance levels 2-5 X as high as the corresponding peak for nulliparous individuals. The exception was site A in 1960, where nulliparous flies also were scarce after the first five-day period. The greater apparent abundance of parous as compared to nulliparous flies would be

explained if a proportion of the *P. mixtum* population was autogenous, so that the parous catch in the second and subsequent five-day periods would consist of females of two distinct histories — those that had completed a gonotrophic cycle after a blood meal and had appeared previously at man or other host as nullipars, and those that had never formed part of the attracted population before, but had completed a first ovarian cycle autogenously. Although dissection of field samples of females throughout the season of the species, as in the present work, cannot provide direct evidence on the question whether certain females of *P. mixtum* can complete an autogenous cycle, there are possible alternative explanations for the greater maximum apparent abundance of parous flies, as well as negative evidence which is given later (page 1137).

If on average a fly spends a greater proportion of its life as a parous individual than as a nullipar, there would be a greater chance, other factors being equal, of catching it in the parous condition. Furthermore it has been shown for other black fly species (Davies, D. M., 1953; Davies, L., 1957b), and has been observed with *P. mixtum*, that only a low proportion, generally less than 25 per cent of females attracted to man at any given time are prepared to bite. Also age-composition studies (Davies, L., 1957c) show that black flies attracted to a cow during a day tend to form a stream of individuals that spend a relatively short time at the host and then depart to be replaced by others. This is in effect a relay system which coupled with the low proportion that bite at any given time, shows that the same individual will often visit one or more hosts more than once before it bites, so that the situation is not incompatible with a greater number of fruitless visits by parous flies than by nullipars, which would contribute to a higher catch of flies in the former condition. However, evidence against this explanation for the excess of parous flies is afforded by the observation that in *Simulium ornatum* Meig. parous flies tended to bite more readily than did nullipars (Davies, L., 1957c).

A potent explanation of the greater apparent abundance of parous as compared to nulliparous *P. mixtum* females, and one which would not imply the occurrence of autogeny in this species, would postulate more rapid dispersal of nullipars from the stream of origin than in the case of parous flies from the stream in which they have oviposited. Direct evidence that this is true in *P. mixtum* is given by comparison of the number of nulliparous and parous flies from May 9 to June 6, 1960 at sites, F, G and H, the topographic positions of which in relation to known breeding sites in the area are shown in Fig. 1. The stream was unsuitable for *Prosimulium* larvae from its origin near site G until it reached site I. The mean number of flies/man/hr. at each site (Table VII) shows that the greater abundance of flies close to the breeding site at F than at either G or H, which were 0.5-1.0 miles from a breeding stream, was largely a result of differences in number of parous flies; nullipars were relatively evenly distributed, while parous flies were far more abundant close to the breeding site. Since sites A-E (Fig. 1) were all close to breeding sites the greater apparent abundance of parous flies (Table VI,a) at each may well largely reflect the concentration of flies in this condition near streams, caused by their less active dispersal relative to nullipars.

P. fuscum. Table VI,b, shows the apparent abundance of nulliparous and parous females, to be compared with the corresponding figures for *P. mixtum* (Table VI,a). Two striking features emerge, namely the consistent rarity of *P. fuscum* nullipars (the highest figure being 8 flies/man/hr., and this was mainly determined by one day's results), and the short season, five to 15 days shorter than in *P. mixtum*, over which flies of this species were attracted to man. The

TABLE VII

Numbers of nulliparous and parous *P. mixtum* at 3 sites, May 9 - June 8, 1960

Site	Flies taken		No. man/hrs. at site	Mean No. flies/man/hr.	
	Nulliparous	Parous		Nulliparous	Parous
F	84	385	9.5	9	40
G	27	81	8.0	3	10
H	29	16	7.0	4	2

peak apparent abundance figure for parous females often occurred in the first five-day period, there being no gradual increase as in *P. mixtum*. In only two cases (site E in 1958, site C in 1960) did appreciable numbers of females occur in the fourth five-day period, and the great bulk of activity was normally concentrated in the first three periods.

The above facts, particularly the abundance and predominance of parous *P. fuscum* in the opening days of the season suggest that the populations studied were comprised largely of autogenous females. Observations were carried out to determine whether this was so and the results are given below.

Direct Observation of Events at an Emergence Site of *P. fuscum*

In mid-April 1959, the stream adjacent to site F (see Fig. 1) was found to contain a vast *P. fuscum* larval population whose identity was confirmed by the cytological examination of many larvae by Dr. K. H. Rothfels and his school (Rothfels, 1956; Basrur, 1959). Frequent visits in April-May were made to this site and the following summarizes the sequence of events:—

April 14 — most larvae were full grown, with black pupal-filament histoblasts indicating imminent pupation.

April 20 — about 20 per cent of the population had pupated.

April 27 — about 90-95 per cent had pupated, male emergence had begun, and a few male swarms were present within 20 yards of the stream.

April 30 — mass emergence of both sexes was in progress, as shown by the presence of hundreds of freshly emerged flies with cloudy wings on rocks and vegetation in and near the stream. Large, loose, male swarms were scattered throughout clearings within 50 yards of the emergence site on this and subsequent days.

May 2 — adult emergence was largely complete, and only a few newly hatched females were seen on stream-side rocks.

May 5 — small numbers of *P. fuscum* females were seen hovering and dipping the tip of the abdomen into the water over the rapids of the emergence site. When seen these females were assumed to be ovipositing in the manner described by D. M. Davies and Peterson (1956), but on dissection all netted specimens proved to be parasitized, either by Microsporidia or mermithid nematodes.

May 7 — many thousands of females performed the hovering-and-dipping procedure over the whole of the rapids at site F, and dissection showed that 68 per cent of 230 netted specimens from these swarms were gravid, most of the remainder being parasitized. For the first time hordes of *P. fuscum* females appeared at man and bit very readily.

May 11, 14, 16, 27 — on the first of these days only, a few females were seen ovipositing, while on the first 3 days *P. fuscum* biting females were moderately abundant, decreasing in abundance from the third to the last day.

In the period May 2-11 numbers of females were recovered from pine trees within 100 yards of the emergence site F by beating the lower branches with a stout net.   These flies were dissected and the stage of development of the lowest follicle in each ovariole ascertained and classified according to the system of Wanson and Lebied (1948).   The results were as follows:—

Ovarian stages	I	II	III	IV	V (Gravid)	Total flies
May 2	30	25	0	0	0	55
May 5	5	6	4	2	0	17
May 7	2	8	4	8	27	49
May 11	32	1	0	0	3	36

Since attraction of females in large numbers commenced on May 7 (in fact only five *P. fuscum* females were taken around man before this date at site F), it became difficult after this date to beat specimens from the trees because the catch inevitably became contaminated from the swarms of flies around the collector. The samples on May 7 and 11 were obtained in early morning and late evening respectively when conditions were too cool for flight (below 42°F.) and so were entirely resting flies.   The flies in stage I and II on May 11 only were all parous individuals, and beating of the same trees on May 27 yielded no *P. fuscum* indicating that the adult season for his species was over for the year at this site.

The above observations and figures show that as soon as emergence of females had occurred to an appreciable extent (May 2), they could be recovered in an early stage of ovarian development from trees close to the stream (intermittent beating of trees 300-600 yards from the stream on various dates yielded no *P. fuscum* females).   Over the six days May 2-7 these resting flies became gravid (stage V), and on May 7 mass oviposition commenced as expected, while on the same day mass biting of man by parous flies began.   The almost complete absence of females around man for five days after May 2 when mass emergence was virtually completed, coupled with the sudden appearance of hordes of blood-thirsty flies on the same day as mass oviposition was first observed, was most impressive.

All these observations show that in these *P. fuscum* populations the females were autogenous.   This was directly confirmed in the laboratory by keeping females reared from pupae alive, feeding them solely on sucrose solution, and observing that after five to seven days at 60°F. most individuals were fully gravid. The occurrence of autogeny in this species thus explains the great preponderence of parous flies in catches obtained by attraction to man (Table VI,b).   That the populations near Ottawa were not exceptional in this respect is suggested by results obtained at McGregor Lake, P.Q., about 30 miles east of site F, when on May 10, 1959, at an early stage in the *Prosimulium* season, 28 *P. fuscum* females dissected were all parous, while only 11 per cent of 72 *P. mixtum* specimens were parous flies.   Furthermore, certain statements in the N. American literature prior to the recognition of the multiple nature of the "*P. hirtipes* complex", and thus all referring to insects under the latter name, can be explained as referring in reality to *P. fuscum*.   Wu (1931) using Michigan material records gravid females among laboratory specimens hatched from pupae and kept alive on sucrose solution. Stone and Jamnback (1955) found that in New York State there was often a delay of several days between emergence and the first appearance of flies at man. Also, Wolfe and Peterson (1958) at Baie Comeau, P.Q., about 450 miles east of Ottawa, recorded ovipositing prior to the first appearance of flies around man. It seems likely from this that *P. fuscum* is autogenous over very large areas of its range in eastern N. America.

TABLE VIII

Proportion of nullipars in three seasons' catches
of *P. fuscum* and *P. mixtum*

		Flies dissected	No. nullipars	% nullipars
1958	fuscum	658	38	5.8
	mixtum	997	367	36.8
1959	fuscum	522	27	5.1
	mixtum	1363	475	34.8
1960	fuscum	2706	79	2.9
	mixtum	5261	907	17.2
1958-60	fuscum	3886	144	3.7
	mixtum	7621	1749	22.9

Occurrence of *P. fuscum* Nullipars Around Man

Despite the autogenous nature of the *P. fuscum* female populations studied, some nulliparous specimens were taken around man by netting attracted flies. Table VIII shows that, compared to *P. mixtum*, the frequency of nullipars was very low, amounting to 3.7 per cent, or 144 specimens among 3886 dissected in 1958-60. These 144 specimens are of some interest, particularly in view of Rubtzov's hypothesis outlined in the introduction of this paper. Bearing in mind the collecting methods used and their rarity, the proportion of nullipars taken in each of the years 1958-60, namely 5.8, 5.1 and 2.9 per cent respectively, was remarkably constant, showing little evidence of variation from year to year, as might be expected to occur if the frequency of autogenous specimens depends on varying levels of larval nutrition as Rubtzov supposes. The ovaries of most of the nullipars were carefully examined for microsporidian parasites, and none were detected, so that they cannot be regarded as largely consisting of parasitized flies with disturbed metabolism, which would otherwise be autogenous. The stage of development of the lowest follicles in nullipars of *P. fuscum* and *P. mixtum* may be compared as follows:—

Follicle stage	I	II	III	Total	per cent stage III
P. fuscum	67	65	12	144	8.3
P. mixtum	1069	650	30	1749	1.7

Although *P. fuscum* nullipars with stage III follicles were scarce (8.3 per cent) they were even scarcer in the corresponding *P. mixtum* females (1.7 per cent), and this difference is highly significant ($\chi^2 = 31.02$, $P = < .001$). The greater frequency of stage III nullipars in *P. fuscum* suggests that some at least of the 144 specimens were autogenous flies that had been prematurely activated to abandon the tree resting sites (page 1126) in which most of this part of the female life cycle is spent. Since autogeny involves not only the triggering off of the metabolic processes involved in complete ovarian maturation, but also the substitution of active flight and host-seeking behaviour by a resting behaviour during the first part of adult life only, it would be surprising if the mechanisms controlling these successively changing behaviour stages did not occasionally get out of phase, so that a fly responds to stimuli which are inappropriate to that particular stage of its development. Among the 30 *P. mixtum* nullipars with stage III follicles, five had unmistakable remains of a blood meal in the mid-gut, ranging from quite a distinct dark red blood mass to smaller blackened remains in an advanced stage of digestion. This suggests that some of the remaining 25 specimens had also had a blood meal but had completely digested it before cap-

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ture. It is therefore likely that the stage III *P. mixtum* nullipars represented individuals that had had an incomplete blood meal, perhaps because of disturbance while engorging. Their rarity would agree with observations that incomplete engorgment in the field is rare in this species, since engorging specimens are very difficult to dislodge from the skin. None of the 12 *P. fuscum* stage III nullipars had any trace of blood in the mid-gut or elsewhere, suggesting that individuals in this stage in the two species, although similar in ovarian development and in the absence of a previous ovarian cycle, are in reality not comparable at all, in the case of *P. mixtum* consisting at least partly of blood fed flies that had had an incomplete blood meal, and in the case of *P. fuscum* probably of autogenous specimens prematurely attracted to man.

In the autogenous *P. fuscum* females obtained by beating the trees on which they rested (page 1126) those with follicles in stage I and II invariably had abundant fat body enveloping the still small ovaries, as well as, in the ventral abdominal region, unhistolysed blocks of larval musculature (these larval blocks were also detected in freshly emerged *P. mixtum* females). In a few of the 132 nulliparous *P. fuscum* attracted to man, with follicles in stage I or II, the small amount of fat body and the absence of larval muscles in the abdomen was most noticeable. This qualitative observation, for what it is worth, suggests that a minority of these flies were anautogenous.

The Rate of Change of the Age-Composition of Field
Populations and the Number of Ovarian Cycles Accomplished

P. fuscum. The observations at site F in 1959 (page 1125) showed that after the oviposition that terminates the first ovarian cycle, females appear at man with very little delay, probably on the same day as they oviposit, if conditions are suitable. Dissection of females attracted to man at F on May 7, 1959, the first day of mass oviposition, showed that in 241 out of 245 specimens the next follicle (i.e. above the follicle relict) was in stage I. In this sample we can be reasonably certain that the flies had oviposited on the day of capture or at the earliest on the previous day, since there was negligible oviposition activity on May 5. Flies captured at man on May 7 and kept alive in the laboratory on sucrose solution showed on dissection five days later that 52 per cent had the lowest follicle, at least in some ovarioles, in stage II. It is concluded that in the field, development of follicles from stage I to II takes place without a blood meal, and that this change requires up to five days in some specimens. If a large batch of females completed the autogenous ovarian cycle on a particular day, one would expect in catches of the resulting parous flies attracted to man, that the proportion with stage II follicles would increase over the next few days, unless more females were constantly completing the autogenous cycle and being added to the attracted population.

Table IX, a, shows the changes in the proportion of flies with stage II follicles in relation to apparent abundance, at site E in 1958. The high apparent abundance of 59 flies/man/hr. on May 6-8 indicates much oviposition in the previous few days, and the low proportion of stage II follicle flies agrees with this. By May 12-15 however the apparent abundance had fallen to 14 flies/man/hr . and the proportion with stage II follicles had risen to over 70 per cent. The latter suggests that little recent oviposition had occurred so that few newly-parous flies had been added to the population, and the fall from 59 to 14 flies/man/hr. in the six to eight day interval could have reflected poor survival of flies. On May 16 apparent abundance rose to 48 flies/man/hr. and was accompanied by a fall in stage II flies to 40 per cent. This suggests that the

TABLE IX

Changes in the proportions of parous *P. fuscum* females with stage II follicles
in relation to apparent abundance

Period	Flies dissected	Per cent with stage II follicles	Apparent abundance (flies/man/hr.)	Per cent of flies with relict eggs
			(a) Site E, 1958	
May 6-8	273	28.5	59	31
12-15	56	71.4	14	32
16	180	40.0	48	19
20	67	11.9	36	13
21-30	42	16.6	c.3	12
			(b) Site A, 1960	
May 9-13	154	37.2	18	15
14-18	43	32.1	7	32
19-28	62	18.7	c.5	16
			(c) Site B, 1960	
May 9-13	135	40.0	45	14
14-18	149	24.5	60	15
19-28	107	17.5	c.25	14

increased apparent abundance reflected a substantial appeatance of newly parous flies.   The maintenance of a relatively high level of apparent abundance on May 20 was accompanied by a further fall in the proportion of stage II flies.

All this is consistent with the conclusion that fluctuation in the size of the catch reflected the successive appearance of females as they completed the autogenous ovarian cycle, and that unless further 'new' flies are added to the attracted population by this process, the apparent abundance of *P. fuscum* females at man after a very few days dropped to a low level, presumably because of fly mortality, following a single wave of oviposition.   Further examples supporting this conclusion are given below.

Table IX,b and c, gives the incidence of stage II flies at sites A and B in three successive periods, showing a decrease in the proportion of flies of this category from one period to the next.   Only the change from May 9-13 to May 14-18 at site B is statistically significant ($\chi^2 = 7.731$; $P = < .01$).   The apparent abundance figures for the two sites at the relevant periods show that at A, flies were rather scarce throughout, but were most abundant in the first period, while at B figures remained high during most of the periods, suggesting continued appearance of newly parous flies on a considerable scale at B only.   In agreement with this the proportion of stage II flies fell significantly only at site B.   In none of the series in Table IX (extreme right column) is there indication of an increase in the proportion of flies with relict eggs in successive periods, suggesting that the flies of each period were consecutively appearing newly-parous flies that did not survive long, and thus the attracted flies were not successive samples of the same and therefore ageing population.   If the latter were true one might expect the proportion of flies with relict eggs to increase with time, since there are reasons for believing that flies that have undergone two ovarian cycles would contain relict eggs more frequently than would flies that have undergone only one cycle.   (These reasons are given below on page 1131).

Table X shows information obtained in 1960 at sites F, G and H (Fig. 1). F is the large *P. fuscum* emergence site mentioned earlier (page 1125), G is 0.5 miles away and H is 1.0 miles.   There were no intermediate breeding sites but larvae of *P. fuscum* were present at the point marked I on Fig. 1, so that females taken at G or H might have come from F or I.   Certainly most of the flies taken at F emerged from the stream alongside, as shown by the evidence on the lack of

TABLE X

Differences in the apparent abundance (flies/man/hr.) of *P. fuscum* females at three sites in 1960. The figures in parentheses are, first the percentage with stage II follicles, second the percentage containing relict eggs

Sites: —	F		G	H
May 9	246		30	162
10	—		65	—
11	654	(16, 11)	—	—
13	1536	(2, 8)	91	24
14	—		592	—
16	808	(11, 7)	—	760
18	321	(8, 14)	—	632
20	31		—	32
24	31	(0, 35)	—	0
30	2		0	0

dispersal of flies during the autogenous cycle (page 1126). Apart from the anomalous figure of 162 flies/man/hr. at H on May 9, the apparent abundance figures in Table X are consistent with a picture of far greater numbers of flies at F than at either G or H until May 14, and thereafter approximately equal numbers at F and H, presumably owing to dispersal of flies from F. If the abundance figures for site F are correlated with those for the proportion of stage II flies, it will be seen that the changes are consistent with the results from other sites already dealt with.

To set the stage for the events behind the figures given in Table X, it should be stated that in 1960 mass oviposition at F started on May 8 and ended about May 14, slightly later than in 1959 at the same site. The rise in apparent abundance from 654 flies/man/hr. on May 11 to 1536 on May 13 (site F) probably reflected the appearance of further newly-parous flies made available by the continued mass oviposition observed at the adjacent stream. As would be expected the proportion of stage II flies fell between the two days from 16 to two per cent. Conversely the fall in abundance to 808 on May 16 and to 321 on May 18 agreed with the observed cessation of oviposition on about May 13, and the proportion of stage II flies rose as expected. The remarkable decrease from 1536 on May 13 to only 31 flies/man/hr. seven days later agrees with the conclusion already stated that unless further newly parous flies are being added, the attracted population of *P. fuscum* quickly drops to low levels after mass oviposition. The abundance figures for sites F and H suggest that this rapid fall was partly an effect of dispersal but the equally low numbers at F and H on May 20 and thereafter suggests that the main explanation is that few flies successfully completed the second ovarian cycle and survive to return to man. In other words, the suggestion is that once females have completed the first ovarian cycle, they suffer heavy mortality, after their first appearance at a host to seek a blood meal for a second ovarian cycle.

The characteristics of females taken on May 20, 24 and 30 at site F suggests that they were the survivors of the large May 9-18 population, and had in fact completed two ovarian cycles, the first autogenous, the second based on a blood meal. The reasons for suggesting this are given below:—
1) All 57 flies dissected for May 20, 24 and 30 had stage I follicles. This cannot have been a result of their being newly parous flies since oviposition had ceased one to two weeks earlier. The development of follicles from stage I to stage II has been shown to take place without a blood meal in about five days in flies that

have undergone *one* ovarian cycle. Presumably this amount of yolk deposition takes place at the expense of materials in other organs of the body, such as the depleted fat body remaining at that time. It is to be expected that in flies that had completed *two* cycles, this limited yolk deposition either would not occur, or would take place rather slowly, since in addition to the even greater depletion of fat body by that time, old age itself would slow up metabolic processes generally. 2) Among the 57 flies, 35 per cent or 20 individuals contained relict eggs, a frequency that is significantly higher than in any previous set of flies at F. For example of 310 flies taken on May 18, 45 had relict eggs. The χ^2 test on these figures gives $\chi^2 = 12.60$; $P = < .001$. A higher frequency of relict eggs in flies that had completed two cycles, than in those that had undergone only one cycle might be expected, not only because increasing age would lead to less efficient ovulation during the second oviposition, but also simply because two-cycle flies would have undergone two ovipositions instead of one.

Some estimate of the proportion of the females that survive the first cycle and appear at man, that then survive the second cycle to appear at man a second time, is possible from the figures given in Table X. This estimate is subject to considerable possible error if only because the apparent abundance figures are not very satisfactory indices of population size at any given time, but are the best that can be obtained at present. If the figures for site F on 11, 13 and 16 May are taken to represent respectively the up-slope, peak and down-slope of the abundance curve of first cycle flies, this gives us a mean of 998 or to the nearest round figure 1000 flies/man/hr. If the flies taken on May 20 and 24 represent second cycle flies as shown above, the latter appeared at a mean rate of 31 flies/man/hr. Thus the estimate is that 100 first cycle flies produced three second-cycle flies. If the corresponding catch figures for site H are used the same result is obtained, namely, three per cent of first cycle flies survive the second cycle and appear at man. If we double this figure to six per cent to allow for the possibility that some second cycle flies died after completing that cycle but before they could appear at man, the figures still suggest that the total eggs laid at the second cycle was probably very small as compared to those laid at the close of the first ovarian cycle in this species. The very low numbers completing the second cycle is in agreement with the rapid fall in apparent abundance in *P. fuscum* after mass oviposition by the autogenous females. We know that the vast majority, possibly all, of the first-cycle eggs will be laid in the same stream and near the same point from which the females emerged, since the autogenous females do not disperse but rest on trees close to their site of emergence (page 1126). The second-cycle eggs may be more widely dispersed since Table X shows that numbers of parous flies were taken one mile from the probable emergence site. The situation in *P. fuscum* therefore seems to imply a rather low degree of mixing of populations in different streams separated by only a few miles, since the second-cycle eggs are so few compared to those of the first cycle. Large samples of *P. fuscum* larvae were collected from the study-area streams and sent for cytological study to Rothfels and his school, whose findings will be published separately. Rothfels (personal communication) states that from preliminary results it is clear that in this species there are considerable differences between the populations in the different streams shown in Fig. 1 in the frequency of certain salivary gland chromosome re-arrangements. This is entirely consistent with the ecological picture outlined above.

P. mixtum. Fig. 2 shows the age-composition of daily catches in the form of 'kites', the catch being classified into parous and nulliparous flies and each of these categories separated into those with stage I and those with stage II follicles.
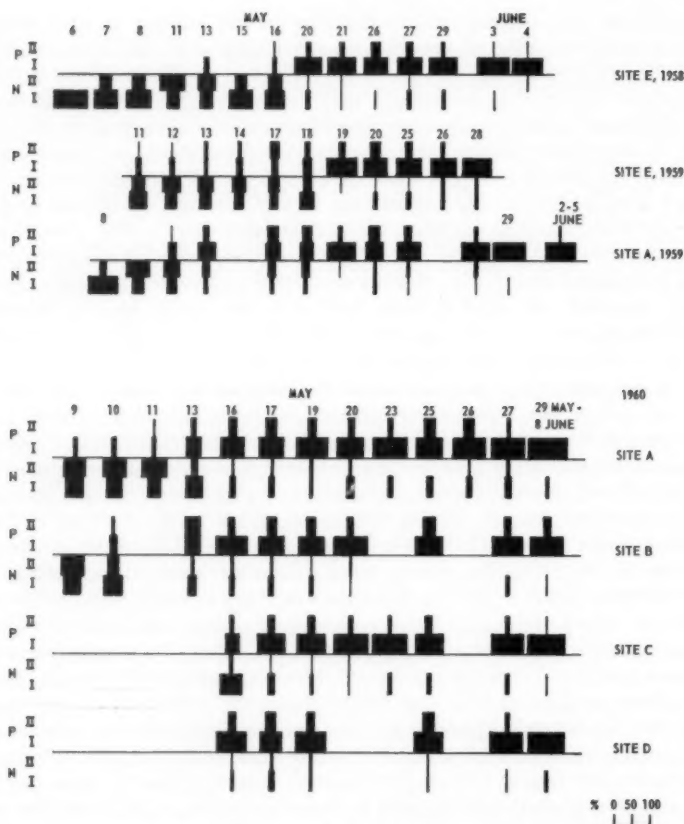
Fig. 2. Age structure of samples of *P. mixtum* females attracted to man on different days throughout the season for this species. Each figure is constructed in terms of the percentages of females of four categories in each day's catch. The four categories are the nulliparous (N) and parous (P) females, each subdivided into those with stage I and those with stage II follicles.

Each 'kite' is constructed on a percentage basis (scale given at right of Fig. 2) so that, for example, the kite for May 9, 1960, site A, shows that the catch was made up of approximately 45 per cent nullipars with stage I, 50 per cent nullipars with stage II and five per cent parous flies, with stage I follicles. This method enables the general age-structure to be compared on different days, and while it does not enable small differences to be shown this is not important since we are concerned with large changes only, smaller changes being in any case probably within the limits of sampling and other errors. A horizontal line is drawn between nulliparous and parous flies to represent the fact that after the first blood meal females will be withdrawn from the attracted population until they reappear, if at all, as parous flies.

Dissection of females freshly emerged from pupae in the laboratory showed that they invariably had stage I follicles. If kept alive for four days at 60°F. after emergence and fed solely on sucrose solution the follicles normally developed to stage II. Only eight flies, however, lived this length of time in the laboratory

out of 63 individuals at the start. Thus this limited follicular development takes place during the first few days of life and does not depend on a blood meal, which is however essential for further oocyte development. In *P. fuscum* it was shown that in parous females the same changes occur, and it is assumed that in the corresponding females of *P. mixtum* also, development of follicles from stage I to stage II takes place without a blood meal. The facts regarding the occurrence of different follicle stages in parous flies in the field agree with this assumption. Nullipars with stage I follicles in the catch are thus likely to have emerged only one to three days previously, so their incidence is a fairly close indication of recent fly emergence. Similarly those with stage II follicles are likely to be at least three days old on capture, and parous flies with stage II follicles may be considered to have oviposited at least three days prior to capture. From the results obtained on *P. fuscum*, however, it is likely that the history of parous flies with stage I follicles is more complex, some being recently oviposited one-cycle flies and others possibly two-or-more-cycle-flies whose last oviposition occurred at an unknown time before capture, and whose follicles have remained in this stage because of age. Other criteria must therefore be sought to distinguish the two-cycle flies, such as the timing of their occurrence in relation to what is known of fly emergence, the frequency of relict eggs as was used in *P. fuscum*, or direct determination of the number of previous gonotrophic cycles by using the number of dilatations on the intima of the ovarioles, as has been done by Detinova (1949) and others for Anopheline mosquitoes.

At the start of the fly season the catch should consist entirely of stage I nullipars, and this condition was fulfilled on May 6, 1958, site E (Fig. 2). Following the appearance and increase of stage II nullipars at this site over the next few days, there followed a decrease between 12 and 15 May, suggesting further emergence. This agrees with the features of larval samples taken about one month previously from the adjacent stream 2 (Table I) which indicated that emergence would be rather protracted there. A similar picture is given at the same site in 1959, while site A in that year showed evidence of a shorter and more discrete emergence since stage I nullipars declined in proportional importance right from the start, showing that emergence was not keeping pace with the ageing of the population. Larval samples from stream I adjacent to site A in 1958 showed that a simple, discrete, emergence would occur, and on April 10, 1959 a single sample from the same place contained the high figure of 68 per cent of full grown larvae, again showing that a discrete emergence would occur. At both sites therefore larval sampling and female dissection results agreed with each other. The occurrence of small numbers of nullipars at site E in 1958 and 1959 until late May (Fig. 2) presumably reflects the continued appearance of small larvae in late winter in stream 2 (Table I).

The metamorphosis of the attracted population from one composed largely of nullipars to one largely formed of parous flies took place remarkably suddenly. Even samples obtained on two consecutive days showed large changes which were permanent and which were reproduced at different sites, for example the changes at sites A and E, 1959, from May 18 to 19 (Fig. 2).

When parous flies first appeared they tended mainly to have stage I follicles, but the proportion of flies with stage II follicles increased for a few days, e.g. site A, 1959 on 12, 13 and 17 May. After a certain date, however, there was invariably a decline in the proportion of stage II parous flies, so that for the last part of the season the parous flies virtually all had stage I follicles. Sometimes there were small changes in the proportion with stage II follicles that interrupted the main seasonal trends, of a magnitude which one would have thought to be prob-

terminal filament

germarium plus quaternary
follicle

tertiary follicle at an early
stage of development

ovariole sheath

tunica dilation of secondary
follicle

beaded connecting stalk

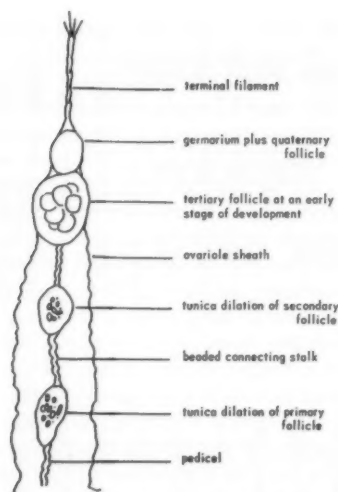tunica dilation of primary
follicle

pedicel

Fig. 3. Features of an ovariole in a *P. mixtum* female, showing that two gonotrophic cycles had been accomplished prior to capture. Approximate scale, tertiary follicle about 40 microns in diameter.

ably less than sampling errors. However, the simultaneous occurrence of these small changes at different sites suggests they were real, although their significance is problematic. For example, the proportion of stage II flies was higher on May 30, 1959 than on the nearest sample dates on either side, at sites A and E. In 1960 at site A, the same category was relatively high on May 25 although it had consistently declined in preceding samples, and at sites B, C and D the same relationships held (Fig. 2). Possibly these minor but reproducible changes were caused by a single age-group being unusually large, as might result, for example, from particularly suitable ovipositing conditions a few days previously.

Attempts to keep numbers of blood-fed females alive in the laboratory to determine the time taken from engorgment to the gravid state failed, so that the length of one gonotrophic cycle is not directly known in *P. mixtum*. However, in *P. fuscum*, netting of autogenous females from trees (page 1126) and laboratory results showed that in that species the cycle takes five to seven days at about 60°F. For the purposes of the discussion below it is assumed that the cycle in *P. mixtum* is of the same duration.

From the last date on which samples contained an appreciable proportion of nullipars it can be roughly estimated when they would have returned in the attracted population as parous flies, by adding eight days to this date. This allows a margin of one to three days for late arrivals, and is probably an even greater margin than this because temperatures to which flies were exposed in the field were certainly higher on average than 60°F., even allowing for cool nights. It is assumed that not more than a day normally elapsed between oviposition and reappearance of the flies concerned at man. This is probably well founded because the vast majority of parous flies on capture had very large follicle relics, comparable to those shown for very freshly oviposited African *Simulium* spp. in Fig. 3, K of Lewis (1960). As shown for *Simulium*, the follicle relics shrunk rapidly in *P. fuscum* and *P. mixtum* when kept alive after capture, being half-sized after one day and as small as shown in Fig. 3 below, after five days. From Fig. 2, at site E in 1958 the last date on which nullipars were abundant was May

TABLE XI

Comparison of certain features of the parous *P. mixtum* population before and after the calculated date on which second-cycle flies became important for the first time. Figures in parentheses express the preceding figure as per cent of flies dissected. Statistically significant differences between pairs using the χ^2 test are indicated by square brackets, and the level of significance as follows:

**, P = <.01; ***, P = <.001

	1958		1959		1960	
(a) Proportion of flies with stage II follicles						
	Flies	No. with stage II follicles	Flies	No. with stage II follicles	Flies	No. with stage II follicles
before	372	58 (15.5)]**	763	211 (27.7)	2880	522 (18.2)
after	252	18 (7.0)]	139	6 (4.3)	987	147 (14.7)
(b) Proportion of flies with relict eggs						
	Flies	No. with relict eggs	Flies	No. with relict eggs	Flies	No. with relict eggs
before	372	39 (10.4)	763	88 (11.6)]***	2880	494 (17.4)
after	252	31 (12.3)	139	35 (25.1)]	987	212 (21.4)

16. Since no samples were dissected thereafter until May 20, let us assume that May 18 was in reality the last day for nullipars. Addition of eight days gives May 26, so that flies taken on and after May 27, 1958 were likely to consist largely of two-cycle flies, if the above assumptions are valid. Error will occur since certainly not all flies taken after May 27 had in fact completed two ovarian cycles, but this would tend to be counteracted by the occurrence of such flies before this date. Proceeding in a similar way for the other series we get a date for the presumed change-over from largely one-cycle to largely two-cycle flies as follows:— 1959 — May 26. 1960 — May 24.

Table XI, b, compares the incidence of relict eggs among parous flies before and after the above dates in each season. Reasons were given (page 1131) for supposing that relict eggs should be more frequent in two-cycle than in one-cycle flies. A doubling of the incidence of relict eggs occurred between the two periods in 1959, and the difference is highly significant ($\chi^2 = 16.83$; P = < .001), while in the other two years a small but non-significant rise occurred. It is reasonable to suppose that factors in the past history of the population, other than the number of ovarian cycles, would affect the incidence of flies containing relict eggs, as well as external conditions such as weather during actual ovipositing activity. If the date of calculated change-over to largely two-cycle flies bears any close relationship to what actually happened in the field in each season, there should be far fewer stage II parous flies after this date than before it. Inspection of Fig. 2 shows that this was so, but since it is concerned with percentages, the actual figures must be examined as has been done in Table XI,a. This shows that as with relict egg frequency the proportion of stage II flies differed markedly between the two periods in the 1959 figures. In 1958 there was also a significant drop in stage II flies, while in 1960 the fall was barely significant.

Estimates of the fraction of first-cycle females that survive a second cycle and return to man, were made by comparing the geometric mean number of

parous flies/man/hr. before and after the calculated change-over dates given above. The results of such a comparison are as follows:—

	1958	1959	1960
(a) Geometric mean parous flies/man/hr. *before* date of supposed change-over	20	19	64
(b) Corresponding mean for period *after* supposed change-over	9	4	9
Fraction of first cycle flies surviving the second cycle, (b) as per cent of (a)	45 per cent	21 per cent	14 per cent

The 1958 figure of 45 per cent survival from the first to the second cycle seems unrealistically high, and suggests that error was involved, presumably because first cycle flies occurred in numbers after the change-over date. The figure of 21 per cent for 1959 seems likely to be fairly accurate because the other evidence suggested that the change-over date in 1959 did achieve a reasonable degree of separation of first from second cycle flies, since differences in the proportions of both flies with relict eggs and with stage II follicles were highly significant (Table XI). In 1960 the auxiliary information on the incidence of relict eggs and of flies with stage II follicles suggests that the figure of 14 per cent survival is not likely to be very accurate.

Discussion

The two species dealt with in this paper are undoubtedly closely related, are sympatric and in fact co-exist in streams of the right type over much of eastern Canada and north eastern U.S.A.; often a single stone bears larvae of both species. Outwardly, therefore, the ecological requirements of the aquatic stages seem very similar, although there may well exist fine differences in larval micro-habitat requirements as suggested by D. M. Davies and Syme (1958); slight differences in the adult emergence pattern where they co-exist agree with this hypothesis. There seems to be an earlier mid-point in the total adult emergence in *P. fuscum* than in *P. mixtum*.

In mixed populations, in spite of the protracted egg hatching season, lasting five months (October-February) or more, adult emergence was highly synchronized so that it occupied three to four weeks in the Ottawa area, and this agrees with information for other parts of eastern Canada (D. M. Davies, 1953; Wolfe and Peterson, 1959). The present work shows that in certain streams an appreciable amount of egg hatching occurred as late as April, after the first pupae have appeared, leading to a longer adult production season than in other streams where spring egg hatching did not occur in detectable amounts. No explanation can be offered at present as to what controls the timing of egg hatch in different streams, but the fact that late hatching did occur has potential effects on the success of control measures, since the standard black fly larvicide used in N. America, namely D.D.T., has a very low toxicity to the eggs and pupae. Since larvicide has therefore to be applied in early spring before pupation starts, incomplete control of *Prosimulium* may occur in streams with late egg hatching, such as stream 2 in the present study.

The major difference between *P. fuscum* and *P. mixtum* appears to be a physiological one, with great ecological consequences, namely the very high frequency of autogeny in the former and its absence or at least its great rarity in the latter. The facts regarding *P. fuscum* are quite conclusive and show that

autogeny is normal in several distinct populations near Ottawa, and statements in the literature suggest that this is true throughout eastern North America. The biting problem in this species therefore is due entirely to the activities of newly parous flies that do not appear to survive long, so that a single wave of flies constitute a problem for about a week only. Where the *P. fuscum* problem lasts longer than this it seems to be due to the successive appearance of waves of newly parous flies, these waves probably being in part a reflection of peaks in the emergence curve. Since *P. fuscum* females did not appear to disperse widely during the autogenous ovarian cycle, the biting problem caused by the resulting parous flies will show marked variations in severity over short distances as was found in the present work. After a single enormous oviposition wave, apparent abundance of parous *P. fuscum* females varied on May 13, 1960 (Table X) between three sites, separated from each other by only 0.5 miles, to such an extent that over 1500 flies/man/hr. were taken at site E, 91 at G and only 24 at H.

The evidence for anautogeny in *P. mixtum* is mainly negative and is for this reason less satisfactory, but may be summarized as follows. A phase characterized by the abundance of nullipars invariably preceded the appearance of parous flies in the field, so that the *P. mixtum* population as sampled in the form of females attracted to man started off the season as an entirely nulliparous one, and changed over the next one to three weeks to one composed largely of parous individuals. This sequence of events is one that would be expected if all or a very high proportion of *P. mixtum* females were anautogenous, and therefore had to appear at man or other suitable host as nullipars to obtain a blood meal necessary for completion of the first ovarian cycle. Further negative evidence for anautogeny in this species is afforded by the fact that while beating trees to recover *P. fuscum* females undergoing their autogenous cycle, no *P. mixtum* females were recovered whose stage of ovarian development could not be accounted for without postulating autogeny. That is to say, the few taken with follicles more advanced than stage II had clear evidence of a blood meal in the mid-gut.

There is some evidence, largely based on the apparently longer-lasting nature of parous populations that a higher proportion of *P. mixtum* females survived a second ovarian cycle than in *P. fuscum*. Autogeny coupled with poor second cycle survival in the one species and anautogeny coupled with better second cycle survival in the other species, must have important effects on the biting problem set up by each. Not only would these differences cause the biting problem constituted by *P. mixtum* to be longer but also would make this species a better potential parasite vector than *P. fuscum* which the present work shows can hardly be of any potential account in this regard. Also at equal population densities in a given area, *P. mixtum* would cause a bigger biting problem than would *P. fuscum*.

Evidence has been presented for the view that nulliparous *P. mixtum* females dispersed more widely from the stream of their origin than did parous females from the streams in which they had probably oviposited. It would appear that in these black flies the main distributive phase occurs in the young females. It follows that if dispersal at this stage is markedly reduced, as has happened in *P. fuscum*, where autogeny seems to involve the settling of the newly emerged females close to the stream emergence sites, a great deal of the whole dispersal power of the species is eliminated. This agrees with the cytological differences between *P. fuscum* larval populations in different streams in the study area separated from each other by only three to 15 miles, compared with the cytological uniformity of *P. mixtum* populations over the same area (Rothfels, personal communication).

The conclusion that parous *P. mixtum* females were far more concentrated near streams than were nullipars seems clear from the figures given in Table VII, and means that at collecting sites near streams, as were most of the sites used in the present work, there would be an excess of parous flies in the overall catches for the season, as was indeed the case (see Table VIII). This situation seems basically similar to that found by Detinova (1953) in *Anopheles maculipennis* in human dwellings where it was termed a 'deficit of nullipars', which Detinova was able to show was a result of the tendency of nullipars to rest away from buildings to a greater extent than later in their life. In *P. mixtum* also the deficit of nullipars appears to have been a result of age-dependent behaviour differences. This however may be only part of the story; it would be surprising if a single collecting technique, namely the capture of flies attracted to man in this case, caught different age-groups with equal efficiency.

The duration of the *P. mixtum* season in the Ottawa area and the admittedly crude estimates of the proportion of parous flies surviving through two ovarian cycles, suggest that a vanishingly small proportion survived a third cycle, and the highest number of ovariolar tunica dilations directly observed was two. The overall picture in this part of Canada is one of relatively poor survival of females when compared with the observed occurrence of up to five ovarian cycles in *Gnus cholodkovski* Rubtz. in Russia (Detinova and Bel'tyukova, 1958). In *P. fuscum* the proportion of flies surviving two ovarian cycles was very low, so that in this species that part of female life after completion of the first ovarian cycle seems much reduced. The situation in *P. fuscum* therefore seems to represent an evolutionary stage intermediate between that in *P. mixtum*, which is fully anautogenous and thus at all stages a biting insect of some longevity, and the condition in completely non-biting species with reduced mouth parts, such as *Cnephia dacotense* D. and S., where a very short life with a single ovarian cycle followed by death of the female is the rule.

The theory of Rubtzov (1955, 1956, 1958) that autogeny in most black flies is influenced directly by environmental conditions, particularly the level of larval nutrition, is not supported by the present work on *P. fuscum* and *P. mixtum*. The occurrence of larvae of these species alongside each other in the same streams, coupled with the very different incidence of autogeny in them, suggest that here autogeny is a species characteristic, although this evidence is not perhaps compelling since there may be differences in efficiency of feeding or some specialization of diet within each species. An argument of greater weight against Rubtzov's ideas is afforded by the very constant apparent incidence of autogeny in *P. fuscum* in each of the three years' work, and by the fact that all streams in the study area, despite their diverse nature, seemed to produce autogenous females. Stream 1 for example (see Fig. 1) drained two lakes, a fact that would be expected to lead to better feeding conditions for *Prosimulium* larvae through the suspended matter derived from the lake plankton. Stream 2 on the other hand had no lakes on its course and so would be poorer in food matter. There is every indication in the present case that autogeny was not simply related to the level of larval nutrition which in turn influenced adult food reserve levels, but is a deep-seated physiological modification probably under genetic control. In well-studied mosquitoes of the *Culex pipiens* complex it has long been known (Roubaud, 1930) that autogeny is under genetic control, and Spielman (1957) recently provided details of the probable distribution of the genes involved on the various chromosomes. The work of Clements (1956), Twohy and Rozeboom (1957) and Chen (1959) clearly show that in these mosquitoes autogeny and anautogeny cannot be explained by differences in the quantities of reserve materials, since

anautogenous individuals contain appreciable reserves but these seem to be destined throughout for purposes other than egg maturation. In *P. fuscum* the present work indicates that a small proportion of females may have been anautogenous. If this character is under genetic control, it may well be that the proportion of anautogenous females may vary from one population to another, in the way that the frequency of various genes is known to vary geographically in those animals whose genetics has been thoroughly studied.

Acknowledgments

Summary

Mixed larval populations of *Prosimulium fuscum* and *P. mixtum* near Ottawa continued to grow to the last instar through the winter in ice-covered streams at water temperatures of 33-34°F. Egg hatching lasted five months or more, while adult emergence was sufficiently synchronized to occupy only three or four weeks. In one stream eggs hatched as late as April causing a longer period of adult production.

P. fuscum larval populations in the streams studied produced autogenous females, and these rested on trees close to their emergence site while they underwent the first ovarian cycle, returning to the adjacent stream to oviposit. The biting problem in this species was concerned virtually entirely with parous females, and this problem did not start until about a week after the end of mass emergence. Probably less than 10 per cent of parous *P. fuscum* females survived to appear at man after completion of a second ovarian cycle. These findings suggest that the species has a relatively slow dispersal rate, so that little exchange of eggs would occur between populations separated by only a few miles.

The *P. mixtum* populations on the other hand either largely or entirely produced anautogenous females that were attracted to man as nullipars soon after emergence started; as the season advanced the proportion of parous flies in the catch increased to exceed 70 per cent in two to three weeks. Over the season as a whole parous individuals outnumbered nullipars at places near streams, while at a site one mile from the nearest suitable breeding place the two groups were equally represented. This suggests that parous flies remained near the streams while nullipars dispersed vigorously thus giving *P. mixtum* a relatively rapid dispersal rate as compared with *P. fuscum* whose nullipars are sedentary.

Crude estimates suggest that about 20 per cent of parous flies survived a second ovarian cycle in *P. mixtum*, compared with less than 10 per cent in *P. fuscum*. This difference, coupled with anautogeny in the former species and autogeny in the latter, indicates that *P. mixtum* is a potential parasite vector while *P. fuscum* is unlikely to be of any account in such a role in the field.

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Life History and Behaviour of the Armyworm, *Pseudaletia unipuncta* (Haw.) (Lepidoptera: Noctuidae), in Eastern Ontario

By J. C. GUPPY

Entomology Research Institute
Research Branch, Canada Department of Agriculture, Ottawa, Ontario

The armyworm, *Pseudaletia unipuncta* (Haw.), has been an important pest of grasses in North America for many years, largely in the eastern half of the Continent, from the more southerly regions of Canada to the southern United States.   The larvae skeletonize the surface of the leaf blades or the inner surface of the sheaths during the early instars, and later feed from the margins of the leaves, consuming all the tissues.   The inflorescence is seldom damaged unless leaf foliage is scarce but in some grasses, notably timothy, the green heads are often readily consumed by the older larvae even when foliage is abundant. Normally, populations of the armyworm are small, attracting little attention, but at irregular intervals of five to 20 years widespread outbreaks have occured simultaneously in Canada and the United States; eight such outbreaks have been recorded since 1860.   In some of the intervening years smaller and more localized outbreaks have occurred.   During the outbreaks, damage to forage grasses and cereal crops has been so severe that the armyworm constitutes one of the most important insects attacking these crops.   The latest great outbreak occurred on the North American Continent in 1954; this was preceded by a smaller but severe attack in 1953, largely in the central United States east of the Mississippi River. In Canada, in 1954, all the provinces from eastern Saskatchewan to Newfoundland were involved.

Before 1954 there were no extensive critical studies on the biology of the armyworm in Canada.   Gibson (1915) briefly outlined the life history of the insect, and Hudson and Wood (1926) reported some preliminary work; however, most important are the detailed reports of past outbreaks by Panton (1896), Gibson (1915), and Baker (1915 and 1939).   Since 1954, Pond (1960) has studied the biology of the insect in New Brunswick.

In the United States, except for the historical work of Riley (1883) and his associates, and the work of Slingerland (1896), most of the critical studies on the insect have been short-term ones conducted during or shortly after major outbreaks.   Recently, Breeland (1957 and 1958) reported on the biology of the armyworm in Tennessee; he gives a review of the previous work in North America and in his 1957 report a bibliography, which when supplemented by that of Riley (1883), offers a nearly complete record of the literature on the armyworm.

Studies on the biology of the armyworm were begun at Ottawa in 1955 and are still in progress.   This paper presents certain aspects of the life history and behaviour of the insect in eastern Ontario as determined in the field, largely in field cages, from 1955 to 1960.

General Methods

Rearing studies were conducted at Merivale, Ont., five miles south of the Central Experimental Farm, Ottawa.   Field observations were made at Richmond, 15 miles southwest of Ottawa, and at Pakenham, 48 miles west.   Light-traps were located at Richmond and at Vernon, 20 miles south of Ottawa.

During this study, eggs of the armyworm were not found in the field and most of the larval populations that were found were small and the larvae in the third, or later, instars.   Therefore, it was not possible to make a thorough study

of the immature stages as they occured in nature.   Accordingly, the insect was studied outdoors in various types of cages.   Each year, the studies were begun with moths captured alive in light traps during the first moth flight in May and June.   The moths were placed in oviposition cages and samples of freshly laid eggs were taken at 2- to 3-day intervals for seasonal-history studies of these and subsequent stages and generations.   Additional information on seasonal development of the larvae was obtained by observing the insect in fields of oats, barley, timothy, and corn.   The durations of the egg, larval, and pupal stages were recorded in conjunction with the seasonal history studies.

The oviposition cages were $24 \times 14 \times 24$ inches in height, having a plywood top and bottom, and sides covered with saran plastic screening; on one side of the cage a 12- $\times$ 24-inch opening was fitted with a nylon-mesh sock.   These cages were used also for fecundity, longevity, and behavioural studies of the moths.

The immature stages were reared in jars or shallow cages that were protected from rain and direct sunlight by means of roof shelters.   Each shelter consisted of a plywood roof, 4×8 feet, supported by four 2×2 inch uprights; these measured 39 inches on one side of the shelter and 35 inches on the other, giving the roof a slight pitch.   Open-frame benches 13 inches high held the rearing containers.   The eggs and early-instar larvae were in eight-ounce glass jars having screened tops; the jars were partly filled with fine sand, moistened periodically to prevent desiccation.   The fourth- to sixth-instar larvae were in wooden-frame cages $12 \times 6 \times 4$ inches deep, having plastic screening on the bottom and on the removable top.   A half-inch layer of sand and sphagnum moss mixed in about equal quantities covered the bottom of the cages to absorb moisture and provide a site for pupation.   Air temperatures in the jars or cages were approximately the same as those in a nearby Stevenson screen.

Larval behaviour was studied on oats or wheat grown in flats, $48 \times 12 \times 6$ inches, in a walk-in plastic-screen field cage similar to that described by Harcourt (1957).   Eggs laid on oat stubble were placed at the base of the plants to create infestations.

Seasonal flight of adults was studied by means of light traps[1] having a General Electric 15-watt black-light fluorescent tube, 18 inches long.   The tube was fitted vertically between four screened baffles arranged at right angles to each other.   A large metal cone below the light tube funnelled the falling insects into a garbage-pail receptacle.

The larvae were fed field-grown oats freshly cut each day.   The moths were fed sugar solution (glucose, 6.25%; fructose, 6.25%; water, 87.5%) contained in a 100 cc. beaker inverted over absorbent cotton in a petri dish.

Life History and Behaviour

Egg

The eggs were laid in narrow bands of a few to several hundred eggs, in two to five rows, rarely in one row.   The numbers of eggs and rows depended on the site on the plant chosen for egg laying.   The individual eggs are more or less globular but being massed together their shape is often irregular; the individual eggs may vary from 0.36 mm. to 0.64 mm. in two or more diameters, the average diameter being approximately 0.54 mm.   The fertilized eggs are pearly white to pale yellow when first laid but in about 24 hours are rather deep yellow.   The egg is lead-grey just before hatching.

In the field shelters, the incubation period of 9,000 eggs varied from three to 33 days, the average in three years' observations being 8.0 days (Table I).

[1]Gardner Mfg. Co., Horicon, Wisconsin, U.S.A.

TABLE I

Duration in days of the immature stages of the armyworm in field shelters,
Ottawa, Ontario, 1957-1959

Stage	Range			Mean			
	1957	1958	1959	1957	1958	1959	3-year
First Generation							
Egg	4–10	6–14	3–10	6.3	9.5	6.6	7.5
Larva	28–35	27–33	24–38	29.8	30.4	29.6	29.9
First instar	3–9	4–6	3–8	4.7	4.9	4.8	4.8
Second instar	3–4	3–4	2–7	3.0	3.4	3.4	3.3
Third instar	3–5	2–4	3–8	3.1	3.2	3.7	3.3
Fourth instar	3–6	3–5	3–9	3.8	3.4	4.3	3.8
Fifth instar	4–7	4–6	2–5	4.9	4.4	4.0	4.4
Sixth instar	9–11	10–13	7–12	10.3	11.1	9.4	10.3
Pupa	19–24	16–24	14–18	21.1	17.8	16.1	18.3
Total	48–54	45–54	39–55	50.9	48.2	45.7	48.3
Second generation							
Egg	5–13	7–33	4–6	7.7	13.1	5.2	8.7
Larva	38–49	53–	21–32	45.6	53+	25.5	
First instar	3–12	8–11	3–4	7.4	8.5	3.2	6.4
Second instar	4–6	4–9	2–3	4.6	5.5	2.2	4.1
Third instar	4–6	6–10	2–3	4.8	5.8	2.3	4.3
Fourth instar	4–9	4–7	2–3	5.7	6.4	2.3	4.8
Fifth instar	5–7	6–9	4–5	6.1	7.0	4.7	5.9
Sixth instar	14–21	22–	7–17	17.0	22+	10.8	
Pupa	60–		23–32	60+		26.3	
Total	98–		46–56	98+		51.8	

Larva

In the field shelters, the larvae typically passed through six instars except an occasional larva that passed through seven. Breeland (1958) reported that in Tennessee some larvae had seven to nine instars when they were exposed to low temperatures in the field during the winter.

Descriptions of the six larval instars are given by Davis and Satterthwait (1916) and Breeland (1958); head-capsule measurements at Ottawa agreed with those reported by these workers. Pond (1960) reported the mean head-capsule widths of the sixth-instar larvae to be 4.75 to 4.88 mm. when the larvae were reared at mean temperatures of 65° F. and 70.7° F.; the mean head width of this instar at Ottawa was 3.34 mm. at similar temperatures.

First instar.–The larvae consumed the egg chorions shortly after hatching and then aggregated in a closely knit mass concealed from view, usually in the site on the plant on which the eggs had been laid. In three instances where the eggs were on a piece of oat stubble from which the sheath had been removed to enable hatching to be observed, aggregating occurred inside the hollow stems. The masses of larvae gave the appearance of being in constant motion due to the wriggling of the outermost larvae. Aggregations of different groups of larvae lasted for 12 to 30 hours on the stubble before the larvae moved onto the host plants to feed; dispersal from the mass occurred during the day or night. Observations suggested that accumulative effects of temperature may determine the time of dispersal.

Following the aggregation period, activity of the first-instar larvae varied to some degree, apparently with the size of the wheat or oat plants that were provided as hosts. On August 9 to 14, 1960, the following pattern occurred in

the field cage on oat plants that were 18 to 24 inches in height: on August 9, most of the larvae dispersed over the plants in the evening and were active until about nine o'clock the following morning. Then, most of them moved under the leaf sheaths. An occasional larva remained on the blades and dropped on a web when the plants were disturbed. For the next four or five days most of the larvae remained in the sheaths where it was difficult to observe their activities. They appeared to feed both day and night. On young wheat plants 6 to 8 inches tall, the behaviour pattern was different from that on the oats: after the initial dispersal the larvae usually began to move up on the plants about 6.00 p.m., and by 9.00 p.m. most of them were on the leaves, usually near the leaf tips where they fed until about eight o'clock the following morning; most were at or near the base of the plant by 9.00 a.m. and were quiescent until evening. This pattern was repeated for four or five consecutive days for each of three different groups of larvae. After the fourth or fifth day the larvae began their first moult. An exception to this pattern occurred one morning: about 90 newly hatched larvae, some that had fed at night and others that had not yet taken food, were near the base of the plants about 8.00 a.m.; between 9.45 a.m. and 10.00 a.m. about 15 of them moved up on the plants and fed during the morning but moved down again by 2.00 p.m. There was no apparent reason for this behaviour.

The wheat plants in this observation were much smaller than the oat plants and apparently the larvae could not gain entrance to the sheath to feed or rest. Between feeding periods some of the larvae rested at the lower parts of the plants, in the longitudinal rolls of the terminal leaves or above the ligule between the blade and the stem; however, during the first two or three days about two-thirds of them moved to the ground between feeding periods and rested in the dry leaves or stubble in which the eggs had been laid. As the first-instar larvae grew older and spread out among the plants fewer returned to the stubble. Riley (1883) reported similar behaviour for the first three or four days of larval life, apparently in natural infestation in the field; when the eggs had been laid in green blades of grass the young larvae remained in these to feed and rest, but when the eggs had been laid in stubble the larvae moved out at night to feed and returned to the stubble for shelter during the day.

The first-instar larvae fed on the upper surface of the green leaf blades, especially near the leaf tips, or on the inner surface of the sheath, consuming all the tissues except the epidermis opposite to that on which they were feeding. An occasional larva fed on necrotic areas in the leaves as did those in the later instars. Although the larvae often fed near each other they did not feed gregariously.

The first-instar larva loops as it moves about, apparently because the first and second pairs of pro-legs are smaller than the others at this stage of development (Davis and Satterthwait, 1916). At the slightest disturbance, the larva drops from the plant on a fine web and hangs suspended and motionless. When the disturbance subsides it regains the leaf in the following manner, as observed microscopically in the laboratory at Ottawa: the web is held between the mandibles and carried downward, where it is grasped by the prothoracic legs and at the same time apparently released by the mandibles; the head then moves in an arc to one side, and simultaneously the mesothoracic leg on the opposite side of the body is moved forward in a wide circle; the mesothoracic leg hooks the web from between the prothoracic legs in circling and carries it back between the meso- and metathoracic legs where it is held between them, apparently on hairs or bristles. The head is erected and the process is repeated, but this time

the head swings to the opposite side and the web is grasped by the opposing mesothoracic leg. As the larvae zigzags its way up the web the meso- and meta-thoracic legs manipulate the accumulation of web into a loose ball. On reaching the leaf the larva crawls away, leaving the ball of web attached to the leaf.

Second to sixth instar.—Behaviour of the larvae in the field cages in the remaining five instars was as follows: they usually fed at night, from dusk until dawn but occasionally some fed in the day time, especially on calm, cloudy days. The larvae fed at all heights on the plant. Early in the second instar the feeding injury was similar to that in the first instar, but as the larvae approached the third instar they often chewed completely through the leaf; shortly before the third instar many of them fed inward from the leaf margins. Larvae in the third to sixth instars always fed inward from the leaf margins, consuming all the tissues. Occasionally, necrotic areas in the leaves were consumed and one second-instar larva was observed to feed ravenously on a rust pustule.

Between feeding periods the second- to fifth-instar larvae rested on the lower parts of the plants, particularly under dead or yellowed leaves. The sixth-instar larvae usually moved to the ground for shelter.

In the last five instars the larvae were not so easily disturbed as they were in the first instar, but when touched they often reared the head and thorax and lashed toward the annoying object before moving away; on the ground they usually curled up when disturbed. According to Riley (1883), and Breeland (1958), the second-instar larva drops on a web when disturbed; at Ottawa this was observed only twice. The second-instar larvae retained the looping movement observed in the first instar. The third-instar larvae either looped slightly or moved with its ventral surface in contact with the plant or ground as in the last three instars; Riley (1883) and Breeland (1958) reported that looping was lost in the third instar, although Riley has described this stage as still having the first pair of prolegs slightly smaller than the others.

When feeding is completed, the sixth-instar larva rests until the alimentary tract has been evacuated and then seeks a suitable location in which to pupate. In the rearing containers the larvae burrowed into the sphagnum moss and constructed cells, which they lined with web; the moss particles, held loosely together by the sparse framework of web, formed a fragile cocoon. In cages that contained only leaves and blotting paper, leaves or paper were often chewed into small shreds and incorporated in a flimsy, oval cocoon, which seldom covered the larva completely.

In the field in 1954 to 1958, if the soil was loose and dry, cell construction was similar to that in the moss in the field cages; if the soil was moist an earthen cell was formed, apparently not always lined with web. Pupae having no apparent cocoon for protection were also found under lumps of soil in the 1954 outbreak or, in 1957, under tight mats of debris between the stems at the base of timothy plants. The pupation niche probably should be considered a cell often lined with web rather than a cocoon.

The durations of the larval instars in field rearing cages from 1957 to 1959 for 25 to 30 groups of 50 to 100 larvae in each of the three years are summarized in Table I; the approximate dates on which the observations were made are shown in Fig. I. The durations given for the sixth instar are from the beginning of the instar until pupation.

In July, August, and early September the larvae ceased feeding about four days before pupation, and in late fall a week to 10 days before pupation.
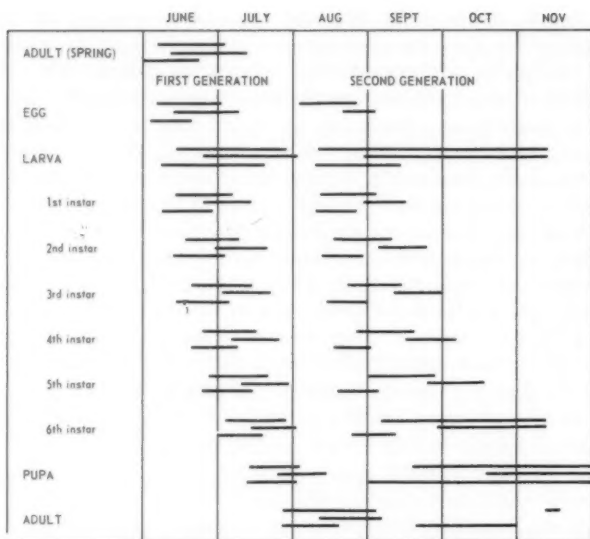
Fig. 1. Seasonal development of *P. unipuncta* based on rearings in field shelters, moth captures in light traps, and observations on larval development in the field. The horizontal lines depict the peak periods of occurrence of each stage; the upper, middle, and lower lines represent the years 1957, 1958, and 1959, respectively.

Pupa

Once the larva begins to construct the pupal cell it also begins to transform to the pupa. The pre-pupal period lasts two to three days in the summer and a week to 10 days in late fall. The larva shrinks in size and turns a dull brown and its segmentation shows more clearly. Shortly before the larval skin is shed the pre-pupa is inactive and appears rigid. The durations of the pupal stage in field shelters are summarized in Table I. Although the pupal-period maximum is given as 60 days, some of the pupae lived more than 60 days in the late fall but apparently succumbed to frost before completing their development.

Adult

Diel behaviour of the moths was studied in the field cages described earlier. The day-time observations were made at hourly intervals. The night-time observations were begun shortly before sunset, and were made for 10 to 15 minutes at sunset and at each hourly interval thereafter until 7.00 a.m., the 12th hour in Table II. To determine the number of eggs laid, dry oat stubble on which the moths had laid was removed from the cages at each hourly interval and replaced with fresh stems. Moths that were feeding were driven away from the sugar solution after each observation. Copulating pairs were not disturbed and their locations in the cages were recorded. In 1958, 60 pairs of moths nine to 12 days old in two cages were observed for four nights, August 19 to 23; and in 1959, 21 pairs of moths seven to nine days old in one cage were observed for three nights, August 11 to 14. Occasional observations were made on other groups of moths at various times.

The moths are inactive during the day. In the field cages they rested motionless, usually shaded by the roof or framework of the cages. Moths that

TABLE II

Numbers and percentages of moths of the armyworm feeding, mating, and laying eggs in field cages at hourly intervals after sunset, Ottawa, Ontario, 1958-1959

Hours after sunset	Moths feeding		Moths in copula		Females ovipositing		Cumulative percentage of eggs laid
	Number	Percentage of total	Number of pairs	Cumulative percentage of pairs	Number	Percentage of total	
0	6	3	0	0	9*	3	
1	22	10	0	0	61	22	19
2	23	10	0	0	57	21	45
3	20	9	0	0	45	17	66
4	28	12	10	21	47	17	83
5	29	13	22	47	23	8	91
6	27	12	40	85	9	3	94
7	21	9	47	100	10	4	97
8	19	8	28	60	7	3	99
9	24	10	14	30	4	1	99.5
10**	3	1	6	13	1	1	100
11	5	2	1	2	0	0	
12	4	1	0	0	0	0	

*Seven of the nine moths were recorded on one day when the sky was overcast.
**The sun rose about 10 hours after it set.

were released during the day usually flew only a short distance before darting to the ground for cover in nearby grass or weeds. During this study only two moths, both females, were observed in the field in the day time. They were in an oat field, resting on stems shaded from the direct sun.

General flight.—In the cages, moth flight began shortly after sunset; it became intense in 20 to 30 minutes and the moths were rather active for about an hour longer. Following the general flight, activity was largely restricted to feeding, mating, or laying eggs. On two or three occasions some of the moths became restless 40 minutes to an hour before sunrise but only for five to 10 minutes before settling down for the day.

Feeding.—Feeding occurred largely between one hour after sunset and one hour before sunrise (Table II). The number of moths feeding increased slightly as the number ovipositing decreased. Only an occasional moth fed during the day.

In late August, 1954, following the severe larval outbreak in July, numerous moths of the armyworm were observed feeding on red clover blooms in the field about 8.00 p.m., 45 minutes after sunset. Feeding continued for about two hours, when the moths suddenly disappeared. On the next day, the writer visited the field but was not able to find any moths in or near the field.

In the cages the moths flew to the drinking fountain, uncoiled their proboscises, and sat quietly as they fed. In the field in 1954, the moths fed on the wing, moving from floret to floret in rapid succession.

Mating.—Mating pairs began to copulate between four and seven hours after sunset. Formation of pairs reached a peak between the fifth and sixth hour after sunset (Table II). In three nights out of seven, mating began just short of the fourth hour and on five nights out of seven it increased up to the seventh hour. Each pair remained in copulation about three hours. Mating began at an hour of the night when egg-laying was diminishing; therefore, mating of females for

the second time probably always occurred after the day's batch of eggs had been laid.

Mating was largely initiated by the males, which fluttered about among the females, apparently willing to mate with any receptive female. When a female was receptive, the male extended his claspers from normally retracted position, approached the female from one side with his abdomen curved toward her, and suddenly clasped her abdomen; he turned away from her at the same time and the two came to rest in the end to end mating position. Occasionally, the male could not withdraw his endophallus after the normal mating period and the pair remained locked together until death; such an aberration is discussed by Callahan and Chapin (1960).

Mating appears to be stimulated by darkness, and four to five hours of darkness appeared to give the maximum effect since mating was at its maximum between the fifth and sixth hour after sunset. Initiation of mating did not appear to be associated with any particular temperature or relative humidity. During the seven nights of observation, the temperature ranged from 76° F. to 52° F. at the beginning of the mating period and 76° F. to 50° F. when mating was at its maximum. Pond (1960) reported that no mating occurred at various temperatures ranging from about 40° to 68° F. but did not state when the moths mated. At Ottawa, relative humidity was 100 per cent during the mating period in six of seven nights observations but was only 70 per cent in one of the nights; except for this one night it was between 90 and 100 per cent two or three hours before mating began.

Both males and females frequently mated two or more times, but multiple mating did not appear to be essential since one female after a single mating laid 1,887 fertile eggs. Callahan and Chapin (1960) found that in moths of the armyworm caught in light traps, multiple matings had been more frequent than single matings.

Egg laying.—Egg laying usually began about 30 minutes after sunset, reached a peak about 30 minutes later, and continued at a high level for three to four hours (Table II). Nine moths were observed laying eggs at sunset, seven of these being recorded on an evening when the sky was heavily overcast. Relatively few moths laid eggs beyond five hours after sunset; this is reflected in the percentages of eggs laid at the various intervals during the night (Table II). About 80 per cent of the eggs were laid in a 3½ hour period beginning about one half hour after sunset. Only an occasional moth was observed laying eggs during the day.

Egg laying appeared to be stimulated by reduced light intensity since in the seven nights it always began about 30 minutes after sunset. Temperature anl relative humidity had no apparent effect on egg laying. Pond (1960) stated that moths did not oviposit at mean temperatures of 60° F. or lower; at Ottawa, the oviposition rate in the field cage was high when the temperatures were in the low 50's and moths oviposited at temperatures as low as 48° F.

When about to lay eggs,the female flew directly to the oat stubble. The moth moved up or down the stem of the stubble with wings partly opened and often vibrating, the abdomen slightly curved forward, and the ovipositor partly or fully extended; she moved her abdomen from side to side, the ovipositor brushing the stem, until she located the open edge of the sheath and inserted her ovipositor. She then quietly laid her eggs, laying the first egg inside the sheath as far as her ovipositor would reach, which was about 3 mm.; she laid the next ones out toward the edge of the sheath, then in again and out once more toward the edge. (In other words, although the eggs are in a band of vertical rows when

TABLE III

Longevity, preoviposition and oviposition periods, and number of eggs laid by the armyworm in field cages, Ottawa, Ontario, July and August, 1956-1959

Number of sexual pairs observed	Average life-span, days		Preoviposition period, days*	Oviposition period, days*	Average number of eggs laid per female
	Males	Females			
In single pairs					
18	19.3**	17.2	6.9	8.7	966.5
In groups of pairs					
10	20.6	15.4	7	11	1,551
10	19.0	16.5	7	13	1,754
13	9.8	14.8	5	12	724
21	18.0	15.5	6	12	1,756
17	17.0	17.3	7	11	1,703
8	16.8	17.6	7	12	1,245
Group mean	16.9	16.2	6.5	11.8	1,451

*Average period given for pairs caged singly; minimum preoviposition period and maximum oviposition period given for groups of pairs.
**Based on 11 males.

found, they are laid crosswise of the band.) She repeated the process row by row, moving backwards down the stem until all her eggs were laid, or until an obstruction such as the junction of the sheath and node interfered with egg laying. If interrupted, she usually moved to another location. The length and depth of the area available on the stem apparently determined the number of eggs laid in any particular location; as many as 400 eggs were laid by a moth in one continuous band. The eggs are held in place by an adhesive that is opaque when wet but crystal clear when dry. The adhesive also serves to seal the egg site, for when the eggs are laid on green or dry leaves it apparently draws the edges of the leaves together, almost completely hiding the eggs.

The writer found that moths given a choice of dry stubble and green plants, with and without dead or dry leaves, usually preferred the stubble and dead or dry leaves to the green plants for egg laying. When only green plants were offered, the eggs were often laid under the sheath at the base of the plants, but more often in the young terminal blades, which were rolled longitudinally. On one occasion a few eggs were laid between two leaves that crossed each other. Insectary observations of Breeland (1958) also indicated a preference for stubble, and even paper strips, over green plants. Observations reported by Riley (1883) suggested a preference for stubble or dry leaves for egg laying in the field. Pond (1960) stated that the eggs are laid singly on blades of grass in the field; this is contrary to the writer's observations and those of Breeland (1958), and Riley (1883) and his associates who apparently observed the eggs in the field in numerous locations.

Longevity and fecundity.—Longevity and fecundity were determined in the field cages. Newly emerged adults were caged singly, or in sexual pairs, or in groups of 10 to 21 pairs. Oat stubble supplied for egg laying was changed daily and the eggs counted. Fresh sugar solution was supplied daily.

Of the single pairs that mated and produced fertilized eggs, the males lived longer than the females, averaging 19.3 days as compared with 17.2 for the females (Table III). The longest life span for males was 27 days, and that for females, 29 days. Moths that laid more than 1,000 eggs lived a few hours to

two days after the last eggs had been laid; those that laid less than 1,000 eggs lived two to nine days after the last eggs were laid. The preoviposition period was 4 to 14 days, averaging 6.9 days; the moths laid 252 to 1,887 eggs per female, averaging 966.5 (Table III). The oviposition period was 3 to 12 days, averaging 8.7. The maximum number of eggs laid in a day by any one moth was 628. One moth laid as many as 1,887 eggs in eight days.

The data on moths caged in groups of pairs are similar to those for single pairs (Table III). However, the moths caged in groups laid one-third more eggs than those caged in single pairs, averaging 1,451 eggs per female as compared with 967. Of the total number of eggs laid by individual females or groups of females the mean percentages laid per day during the oviposition periods were:

Day of oviposition period	1	2	3	4	5	6	7	8	9	10-13
Percentage of eggs laid,										
individual females	13	20	20	11	9	10	8	6	2	1
groups of females	3	10	14	16	15	15	11	8	3	5

Moths of both individual pairs and grouped pairs laid most of their eggs over a seven-day period.

For reasons unknown, one-half of the pairs of moths caged individually, 18 pairs in 36, produced no eggs or a few that showed no development at all. The life span of the moths that laid none or very few eggs was rather variable; males lived 7 to 41 days, averaging 22.5, and females 11 to 45 days, averaging 24.5.

Unmated females caged alone usually laid none or very few eggs but one moth laid 127 eggs over a 13-day period, and another laid 470 eggs over a 10-day period.

Twenty-five male and 25 female moths were caged in single pairs or in groups of pairs, and given water instead of sugar solution. Both sexes lived for 5 to 19 days, averaging 14 days. The females laid 6 to 46 eggs, averaging 2.9 per moth, but none of the eggs was fertile. Apparently food is required for normal egg production, and possibly for mating.

Seasonal History

Early-summer development of the armyworm in eastern Ontario begins with moths that the writer at present considers to be migrants that overwinter in the more southerly regions and migrate north in the spring; the first moths appeared in the light traps as early as May 18 but were never abundant until June.

Light-trap captures of moths indicated that two main flights occurred each year. The flight periods and the number caught in two traps in four years were:

	First flight	Number captured	Second flight	Number captured
1957	May 20—July 10	342	July 25—September 30	100
1958	May 22—July 15	130	August 12—September 23	14
1959	May 18—July 10	36	July 21—August 18	20
1960	May 26—June 3	9	July 16—August 2	14

In 1959, five moths were caught between September 9 and October 9, which were presumably of a third flight (second generation); in the rearing studies moths of the second generation (third flight) emerged between September 10 and October 26. The peak periods of the first flight based on the light-trap captures, and those of the second and third flights (first- and second-generation adults) based on the trap captures and rearing studies, are depicted in Fig. 1.

In each of three years, 1957 to 1959, 25 to 30 groups of 50 to 100 eggs of the first and second generations and their successive stages were observed in the field shelters.   The studies were begun in late May or early June and continued until freeze-up.   They, and observations in 1955 and 1956, indicated that two complete generations of the armyworm occur annually at Ottawa (Fig. 1) and occasionally a partial third.   The first generation occurred from late May to August and the second generation from early August to October or November. In 1957, only 60 per cent of the second-generation larvae transformed to pupae, and only about 15 per cent of the pupae gave rise to moths in that fall.   In 1958, about 25 per cent of the second-generation larvae transformed to pupae but none of the pupae gave rise to moths before freeze-up.   In 1959, all of the second-generation larvae transformed to pupae and 65 per cent of these gave rise to adults; this resulted in a partial third generation in late September and October. In 1959, eggs of the third generation were laid in late September and early October but those laid after October 1 failed to hatch; a few larvae reached the second instar by mid October but then succumbed to frost.;

Seasonal development in 1955 and 1956 was similar to that in 1957 and 1958, respectively.

In past outbreaks of the armyworm in Ontario, the damage was almost always done by the brood of larvae that appeared in July and early August (Gibson, 1915).   In the 1954 outbreak, the first report of larval damage in eastern Ontario was on July 8, and the last report about August 3.   This coincides with the peak period of the sixth instar, first-generation larvae, in the three years' seasonal-history studies at Ottawa.   Hence, the seasonal-history data and the writer's observations during the 1954 outbreak suggest that it is the first-generation larvae that have caused the damage in past outbreaks and that most of it has been done by the sixth instar.

In the State of Mississippi the moth apparently breeds throughout the winter months (Moran and Lyle, 1940).   From Tennessee northward as far as New York State, the armyworm passes the winter as partially grown larvae (Breeland, 1958; Davis and Satterthwait, 1916; Slingerland, 1896; Knight, 1916). The adults have been reported to winter in New Jersey (Slingerland, 1896) and in Ohio (Webster and Mally, 1898).   However, there is evidence to suggest that the armyworm does not overwinter at Ottawa.   In the field shelters, sixth-instar larvae survived only until early November, and the first- to fifth-instar larvae only until late November.   Some pupae gave rise to adults as late as mid-November but pupal survival beyond this time was not determined.   During October, 1956 and 1957, approximately 1000 larvae, some of them in each of the six instars, were placed in hibernation cages covering natural grassy areas or bare soil; some of the mature larvae burrowed into the sod or soil and transformed to pupae.   Only dead specimens were found in the following spring.   In 1959, second-generation adults that emerged in late September and early October laid eggs and died after a normal life span.   Moths emerging in November, 1957, died shortly after emergence; however, it is possible that in nature these moths might have found shelter, and hibernated.   Many of the moths captured at light traps in May and early June were perfect specimens and appeared to be freshly emerged, although, since they were usually gravid, at least several days old.   The first moth flight began about the same time each spring regardless of local weather conditions, further indicating that the moths do not overwinter locally. It is perhaps of significance that the duration of the first flight of moths at Ottawa, late May to early July, coincides with that of the second flight of moths in Tennessee (Breeland, 1958).

Host Relationship

Although the armyworm has been reported as feeding on a great variety of both mono- and dicotyledonous plants (Breeland, 1958), it normally feeds on grasses. Reports of damage during outbreaks suggest that cultivated hosts are preferred, especially the small grains. In Canada, during the great outbreaks of 1896 and 1914, Panton (1896) and Gibson (1915) reported that about one-half of the infested fields were oats; in 1896, the other infested fields were largely corn and wheat and in 1914, corn, barley, and hay or pasture grasses. In eastern Ontario during the 1954 outbreak, most of the infestations were in oat fields, although timothy and other crops were attacked. Hence, in the outbreaks in Canada, the armyworm seemed to prefer oats. Maturity of the host plant, density of stand, stubble or dead leaves for egg laying, and probably other factors in combination or alone may, however, be more important in attracting the insect than is host species. In the few infestations observed from 1955 to 1959 at Ottawa, the various crops appeared to be attacked in a definite time sequence. Larvae found in timothy matured about 10 days earlier than those in oats or barley and five days earlier than those in corn; larvae in corn matured about five days earlier than those in oats or barley. In eastern Ontario in 1954, damage to timothy was reported about 10 days earlier than was damage to oats.

Summary

In studies on the armyworm, *Pseudaletia unipuncta* (Haw.), at Ottawa, Ont., 1955 to 1960, in field cages, adult activity began shortly after sunset and continued through most of the night. An intense general flight began about 30 minutes after sunset and lasted about an hour. The moths fed mainly from one hour after sunset to one hour before sunrise. Mating was at its peak between five and six hours after sunset and each pair was in copula about three hours. Multiple matings occurred in both sexes. The peak period of egg laying lasted about 3½ hours and began about one-half hour after sunset. The eggs were laid in narrow bands of a few eggs to several hundred, in 2 to 5 rows. They were laid under the sheath, or in folds in the leaf blades, of grasses, and on the dry stubble or dead leaves of the grasses in preference to the green foliage.

When sexual pairs were caged singly the males lived an average of 19 days and the females 17 days. The preoviposition period averaged 6.9 days. The moths laid 252 to 1,887 eggs, averaging 967, most of them in a seven-day period. Moths caged in groups of pairs laid one-third more eggs than those in single pairs. The incubation period of the eggs was 3 to 33 days, averaging 8.

The newly hatched larvae fed on the egg chorion and then aggregated in the site on the plant where the eggs had been laid; after 12 to 30 hours they moved to the green leaves or sheaths to feed. In the field cage, larvae of all six instars fed mainly at night. The first-instar larvae fed on the upper surface of the leaf blades or on the inner surface of the leaf sheath; between feedings in the first few days most of the larvae that fed on the leaf blades returned for shelter during the day to the area on the plant where the eggs had been laid, but those under the sheaths remained under them 24 hours a day. The second-instar larvae ate only the surface of the leaf at first, but as they approached the third instar many of them ate all the leaf tissues from the margins inward, as did those in the last four instars. The second- to fifth-instar larvae rested under the lower leaves in the day-time, and those in the sixth instar moved to the ground for shelter.

In the three years 1957 to 1959, the duration of the larval stage, first generation, in June and July, averaged about 30 days; that of the second generation, in

August and September, was 25 to 45 days. The duration of the pupal stage averaged 18.3 days in mid summer and was 23 to 60 days in the fall.

In the field cages, two generations of the armyworm occurred annually and once in the six years of the study there was a partial third generation. The first-generation larvae occurred from early June to early August, and the second-generation larvae from mid August to mid October.

Seasonal-history data and the writer's observations during the 1954 army-worm outbreak indicate that it is the first-generation larvae, particularly the sixth instar, that have caused the damage in past outbreaks in Ontario.

Evidence to date suggests that the insect does not hibernate at Ottawa.

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A 40-Cubic-Foot Air-Conditioned Cabinet[1]

By C. JACKSON

Chemical Control Section
Ottawa, Ontario

Small, inexpensive air-conditioned cabinets that are easy to construct, maintain and adjust, are needed in many laboratories. Commercially available equipment is not specifically designed to maintain moderate and precise conditions for long periods.

This paper describes the design and physical performance of a laboratory air-conditioned cabinet 40 cu. ft. in volume with a miniature air-conditioning system fitted to it. Air motion and distribution as well as temperature and humidity are precisely controlled. Temperature can be held at any desired level from 65 to 85 ± 0.5°F. and humidity from 45 to 85 per cent with accuracy of ± 1 per cent R.H. provided the ambient conditions are from 65 to 85°F. and 5 to 85 per cent R.H.

This air-conditioning unit is an improved version of that described in an earlier paper by the author (Jackson, 1960). A separate dehumidifying system is used and one 15 amp. outlet is required; no water and sewer connections are necessary. It can be constructed from readily available equipment and materials with the exception of the air cooling coils.

The work was carried out at the Entomology Engineering Shop, Ottawa, and a considerable number of modifications from the original design were incorporated and tested.

Gross Features

Fig. 1 shows the main working parts. The unit comprises essentially a cabinet (1) with a large quadrate funnel (2) and perforated diffusing panel (3) installed in it. The cabinet is mounted on a stand (35); under the cabinet is the air-conditioning unit (4), and transition ducts (9, 10) connect the ends of the unit to the cabinet by elbow and exhaust fan (11).

The unit contains lamps (5) for heating, an open water pan with immersion heaters (7) and damper (8); for humidifying, two water-cooled coils (6) are used for cooling the air; they are supplied with water by two water immersion pumps (23) from a tank of water (24) which is cooled by a refrigeration plant (25) that is installed behind the air-conditioning housing. The box (14), with the exhaust fan (13) connected to it and the tray 'of silica gel (15) suspended in it, constitute the dehumidifying apparatus. It is disconnected from behind the water cooling plant when the air-conditioning cabinet is moved.

Fastened to the mounting board (28) is the electronic control panel and modulating motor combined (20), for heating, cooling, humidifying, and dehumidifying panel and motor (27, 29), transformers (30, 40), temperature selector (39), mercury contact switches (22), and cams (21), to activate them. Coloured pilot lights (32) show what the thermostat (19) and humidistat (26) are calling for, which help to set up and maintain the apparatus.

The Cabinet

The cabinet (1) is 28 in. wide, 75½ in. long, and 48 in. high, in outer dimensions. It is constructed in panels, the top and bottom are constructed full size, and the walls are fastened between them.

Two doors (33), 23 in. wide, 40 in. high, one with a window (34), are installed in the front wall of the cabinet. Covering the entire end wall, inside the

cabinet, and ¾ in. away, is an air diffusing panel (3), ⅛ in. thick with 194 holes, ⅛ in. in diameter, spaced evenly over it, except in the centre directly opposite the 4 in. duct orifice. Twenty inches from the other end wall the base of a large quadrate funnel (2) is fastened with its apex tapering to a 4 in. hole centred in the wall.

Stand, Housing and Ducting

The stand (35) is 28 in. wide, 75 in. long, 30 in. high, including casters.

The air-conditioning unit housing (4) is 8 in. wide, 6 in. high, and 60 in. long. It is connected to the 4 in. holes in the ends of the cabinet with transition ducts (9, 10), elbow, and a 235 cu. ft. per min. exhaust fan (11). Access doors (36, 37) to the heaters, humidifier, and air-cooling coils, are in the side of the housing; one opening is 14 in. long and the other is 28 in. and both are 6 in. in height and covered with ⅛ in. clear sheet plastic.

Heating, Cooling, Humidifying and Dehumidifying Apparatus

The six 25-watt lamps (5) for heating are installed in two electrical circuits. The two coils (6), to cool the air, are 7½ in. wide, 12 in. long, and 5¼ in. high; each coil is supplied with water by one of the two pumps (23) that are installed in an insulated tank (24) that holds 14 gal. of water, chilled by a ¼ H.P. refrigeration plant.

An open water pan (7), 3¼ in. wide, 7 in. long, 2½ in. deep, that is supplied with water from a tank or pressure system, is used for humidifying. Installed in it is a simple adjustable overflow device and two 250-watt heaters; their output is controlled by variable transformers (30). When extreme conditions are not required, one 100- and one 200-watt Glo-Quartz radiant heaters may be used without transformers. A 2½ in. hole is in the cover for the pan which has a steel-hinged damper (8) to close it.

For dehumidifying, 20 lb of ⅜ in. mesh size silica gel (15) is held in a 14-mesh copper screen basket which is placed in a sheet-metal-lined box (14), 12 in. wide, 22 in. long, 14 in. high, in outer dimensions, so that the air must pass through the silica gel. An 85 cu. ft. per min. exhaust fan (13) is connected to one end of the box and the 3 in. duct (12) connects to duct (10). The 3 in. duct (16), is connected to the other end of the box and to the housing of the unit between the humidifying damper (8) and the lamps (5); a piston type damper (17), is installed in this duct.

Air Distribution

The air is drawn continuously from the cabinet (1) by the fan (11) and passed through the air-conditioning housing (4) where it is cooled, humidified, or heated, then passed into the air mixing plenum chamber (18) where it is mixed and released evenly through holes in the diffusing panel (3). It then passes slowly at 25 F.P.M. through the cabinet and is gathered up by the large quadrate funnel (2) which also feeds the fan (11) properly. When dehumidifying is required, some air is drawn from duct (10) by the exhaust fan (13) and passes through the silica gel (15) through duct (16) and is then released by the piston type damper (17) into the air-conditioning housing (4) completing the bypass.

Controls

The controls are practically the same as those described in 1960 (Jackson, 1960). When the electronic thermostat (19) calls for heating or cooling, it activates a reversing, modulating motor (20) that turns in one direction for heating and in the other for cooling; the number of degrees the motor turns depends

on the magnitude of the signal from the thermostat. Four adjustable cams (21) are connected to the axle of this motor which move electrical mercury contact switches (22) when the motor turns, first turning on one circuit of lamps for heating, and then the other circuit for extra heating when the signal is strong enough. These circuits are wired into the switches.

When the thermostat signals for cooling, the modulating motor (20) reverses and starts the pumps (23) that supply the chilled water to the air-cooling coils in the same proportioning way as the heating.

The humidistat (26) that controls the humidifying and dehumidifying through the control panel (27) and the modulating motor (29) has three cams connected to one end of its axle to activate three switches: two for water heaters, and one for the exhaust fan. At the other end of the axle, is a crank-arm (31) that is connected to the damper (8) covering the open water pan and to the piston-type damper (17) which releases dry air from the dehumidifying box (14).

When adiabatic conditions are reached, the arm (31) is in its neutral position and both dampers are closed. When the humidistat sends a weak signal for humidity, the motor rotates 5 degrees; this movement opens the damper slightly and turns on one heater in the open water pan. When a stronger signal is received, the motor turns another 5 degrees causing the damper to open more and the second heater to operate.

The dehumidifying piston type damper (17) is controlled in the same way; when the motor rotates, the switch turns on the exhaust fan (13), opens the damper, which releases dry air, and when the signal increases, the damper opens wider and releases a greater volume of dry air.

The temperature of the water that is pumped to the air cooling coils is controlled by a thermostatic expansion valve on the refrigeration plant. To prevent condensation on the air-cooling coils, this water is chilled only 3 to 5°F. below the dew point of the air in the cabinet.

Materials Used

Cabinet: Two inch by 2 in. lumber is used for the frames of the panels and doors; these are covered with aluminum foil, then with ¼ in. plywood and interlined with 2 in. glass fibre insulation. Expanded polystyrene insulation which is very light, inert, and fungus-resistant, may also be used. All joints between panels are sealed with caulking compound. Three-quarter-inch plywood, ⅜ in. overlapped, covers the outer side of the doors, so that refrigeration gasketing and hardware can be used. The window in the door is triple-glassed, ⅛ in. composition board is used for the air diffuser, and ½ in. plywood for the quadrate funnel.

Stand: Two pieces of ¾ in. plywood are used for the top and bottom of the stand, held apart with 4 in. by 4 in. lumber. Seven-inch metal corner brackets support

Fig. 1. Elevation Diagram Drawing of Apparatus and B, Cam. C, Mercury tube. D, Switches. 1, Cabinet. 2, Quadrate funnel. 3, Perforated diffusing panel. 4, Air-conditioning unit housing. 5, Heaters. 6, Air-cooling coils. 7, Float-operated open-water pan. 8, Damper. 9, 10, Transition ducts. 11, Exhaust fan. 12, Duct. 13, Exhaust fan. 14, Air drying box. 15, Silica gel. 16, Duct. 17, Piston type damper. 18, Air-mixing plenum chamber. 19, Thermostat. 20, Temperature control panel and reversible modulating motor. 21, Cams. 22, Mercury contact switches. 23, Immersion pumps. 24, Water tank. 25, Refrigerant plant. 26, Humidistat. 27, Humidity control panel. 28, Mounting board. 29, Reversible modulating motor. 30, Transformers. 31, Crank arm. 32, Coloured pilot lights. 33, Doors. 34, Window. 35, Stand. 36, 37, Access doors. 38, Lumber. 39, Temperature selector. 40, Transformer.
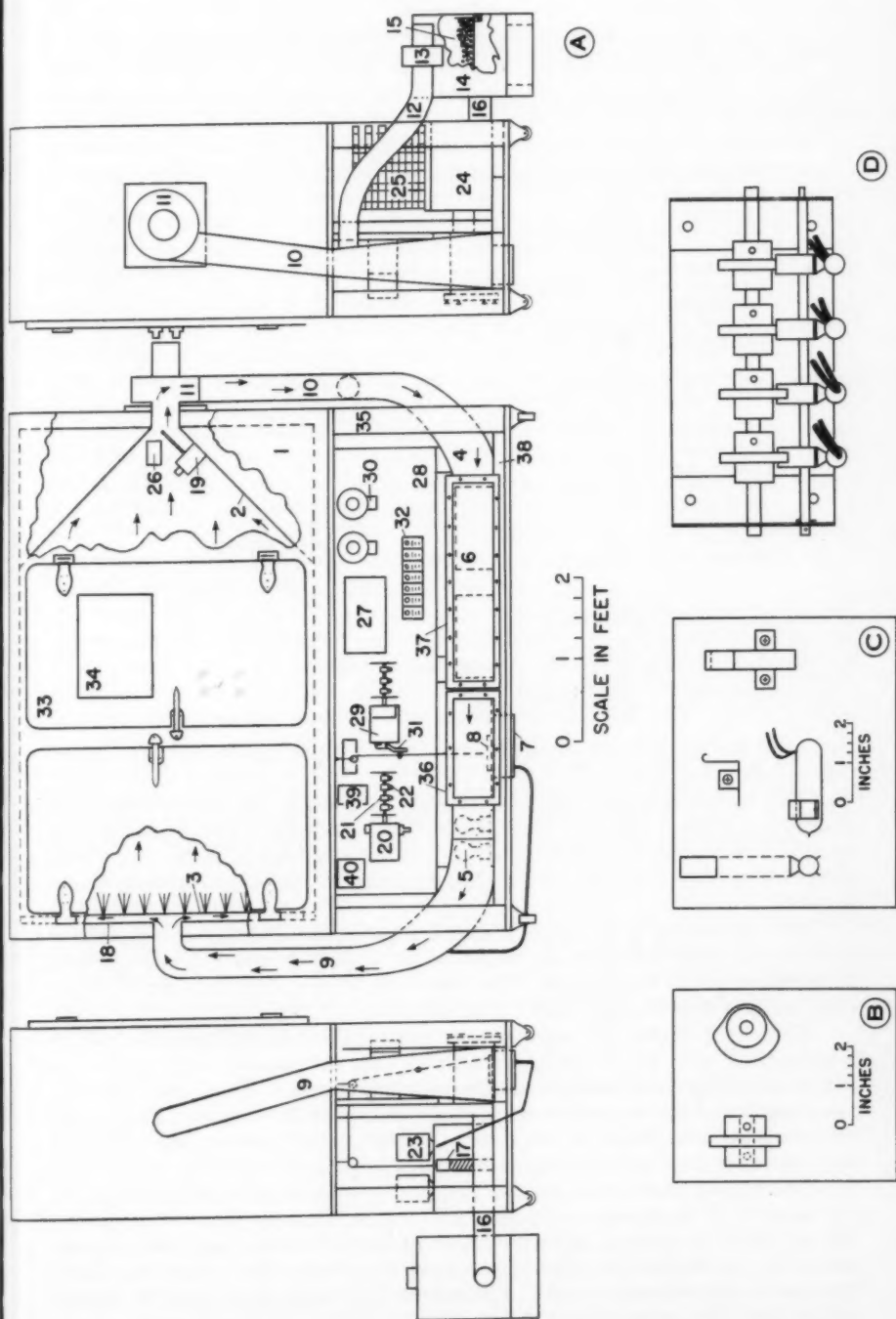
TABLE I
Commercially available equipment used

Ref. number (Fig. 1)	Description of equipment	Company	Catalogue number
20	Electronic and panel combined modutrol motor	Honeywell[1]	M7021A
19	Insertion thermostat	,,	L7004A1
39	Temperature selector	,,	Q406A1
27	Relative humidity control panel	,,	MD55147A
29	Reversible modulating motor	,,	M904F30DS
26	Electronic humidistat	,,	H7000A2
26	Electronic humidity sensing element	,,	Q229A7
40	Transformer	,,	AT72D2CG
22	Mercury contact switches	,,	AS454A
	Two switch auxiliary switch	,,	Q52E
	,, ,, ,, ,,	,,	Q52F
	Multiple step auxiliary switch	,,	S416
11	Exhaust fan 235 cu. ft. per min.	D. S. Fraser[2]	
13	,, ,, ,, 85 cu. ft. per min.	Kresno-Stamm[3]	BL1
6	Air-cooling coils	Keep Rite Products[4]	
23	Immersion pump	Canlab[5]	72-806
30	Transformer	,,	32-072
	Glo-quartz radiant heater	,,	42-645
	Dehumidifier	Desomatic[6]	SOR-8
	Demineralizer	Canlab	30-865
15	Silica gel	McArthur Chem.[7]	
	Copperline wall Hi-fin	Unifin Tube[8]	

[1] Honeywell Controls Ltd., Leaside, Toronto 17, Ont.
[2] D. S. Fraser and Co., 92 Isabella St., Ottawa 1, Ont.
[3] Kresno-Stamm Manufacturing (Canada), Montreal 24, P.Q.
[4] Keep Rite Products Limited, Brantford, Ont.
[5] Canadian Laboratory Supplies, P.O. Box, Stn. St. Laurent, Montreal, P.Q.
[6] Desomatic Products Inc., 1109 West Broad St., Falls Church, Va., U.S.A.
[7] The McArthur Chemical Co., 1396 St. Patrick St., Montreal 22, P.Q.
[8] Unifin Tube Co., P.O. Box 7, 1109 York St., London, Ont.

the legs. The bottom of the stand is covered with 1¾ in. lumber (38) for insulation and extra support.

The air-conditioning apparatus housing and ducts are constructed with 28-gauge galvanized iron and covered with 2 in. insulation. The frames for the access doors are mild steel angle ⅛ in. by 1 in. by 1 in., and ⅛ in. by 1 in. Flat, clear sheet plastic, ⅛ in. thick, is used to cover them. This is held on with thumb screws.

The air-cooling coils can be obtained from a manufacturer or constructed with two 24-gauge copper tanks 1⅜ in. wide, 12 in. long, and 5¼ in. high, with 22 pieces of ⅝ in. O.D. copper wall 0.04 thick, Hi-fin, eight fins per in., 5 in. long, and soldered into the tanks 1½ in. on centre.

Three-inch flexible ducting is used to connect the dehumidifying box, which is constructed of ½ in. plywood, to the unit. One and one-half inch copper pipe and brass plunger are used for the piston type damper. The ¾ in. plywood mounting board for the electronic controls, etc., is 65 in. long, and 15 in. high, supported by three pieces of 2 in. by 4 in. lumber, which are fastened to the top and bottom of the stand with their 4-in. sides up against the housing.

The mercury switch mechanism (21, 22) consists of two parallel shafts, the top one is ⅜ in. in diameter and supports 1 13/16 in. diameter cams. The bottom one is 3/16 in. in diameter and is installed 1 in. away from the top shaft and supports the cam followers which are weighted so that they follow the cams. Fastened to the followers are the clips and mercury contact switches. Drawings of cam and follower are shown in Fig. 1 B, C and D.

Discussion

The operation of the unit described above has been most satisfactory for two years. However, as with most controlled units, the humidifying system has occasionally malfunctioned because of mineral deposits in the open water pan. This difficulty can be eliminated if the pan is cleaned out when necessary or a demineralizer used.   The automatic electronic controls have functioned perfectly. The sensing elements will respond to fractional changes in their environment and control the modulating motors in proportion.   When the motor switches on the heating or cooling, the results are not drastic and there is no overshoot, but dampers are required for the humidifying and dehumidifying apparatus to minimize overshoot when the throttling range is set for ± 1 per cent R.H. or less.

The construction of the cabinet, housing, and ducts is reasonably air-tight, but would have been better tighter, because the difference in the vapour pressure within the cabinet and ambient pressure is considerable at different times of the year.   This causes the humidifying apparatus to work quite often when holding the environment to ± 1 per cent R.H. or less.   The same condition will prevail if the exhaust fan is over-sized; pressure will be increased in the cabinet and air will leak out.   If the exhaust fan is not large enough, however the air will short circuit and stable conditions will be impossible to maintain.   The cooling system is large enough to maintain conditions if ten 40-watt fluorescent lamps, 48 in. long, are used to light the cabinet.   The top panel of the cabinet is replaced by two pieces of glass, held ¾ in. apart, the lights are installed 12 in. above the glass, and will give about 1200 ft. candles of light.

While this is a lot of apparatus to maintain an environment, it must be understood that any complete air-conditioning system has a summer and winter cycle.   The winter cycle involves heating and humidifying; cooling would not be required unless lamps were being used to light up the cabinet or if an environment was being maintained lower than ambient temperature.   In summer, cooling is required and dehumidifying only if a low R.H. is being maintained.   The dehumidifying apparatus on the unit is not necessary if a mechanical or commercially available chemical absorber is used to dry the ambient air a little.   If tests could be conducted when the R.H. is not high (where it is high in an area only for a few weeks in any one year) dehumidifying would be unnecessary.

The design of the air-cooling coils and mercury contact auxiliary switches is given because these items are easy to construct, and the switches are simple to adjust.   Thirty of these switches can be operated from one end of a reversing, modulating motor and could be used to control many different types of air-conditioning apparatus. The cost of materials and equipment, including refrigeration plant to construct this smoothly functioning unit, need not exceed $1200.00 (1959 prices).

Summary

The description of the design, operation, performance, construction details, and materials used for a 40 cu. ft. portable cabinet, with controlled temperature, humidity, and air distribution for a constant and continuing environment, has been given.   The air is gathered up evenly in the cabinet by a large quadrate funnel, then forced by the fan through air-cooling coils which are cooled with water and over an open water pan with immersion heaters in it to humidify. Then the air passes around the lamps that are used for heaters and enters an air-mixing plenum chamber from which it is released over the entire end of the cabinet through a perforated diffusing panel.   Some air is drawn off the main stream when dehumidifying is required, and forced through silica gel to dry

before entering the mixing plenum. Electronic controls are used to operate the apparatus, which has successfully produced a constant environment during a two-year testing period.

Acknowledgments

I wish to express my sincere thanks to John K. Campbell, Assistant Technician, Entomology Research Institute, for maintaining the air-conditioning apparatus. I also wish to thank Dr. J. J. Fettes, Head, Chemical Control Section, for his assistance and constructive suggestions in regard to the manuscript.

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Polygyny in *Choristoneura* Led. (Lepidoptera: Tortricidae)[1]

By I. M. Campbell

Section of Cytology and Genetics
Forest Insect Laboratory, Sault Ste. Marie, Ontario

Introduction

In adult populations where females are in excess of males, the ability of the males to mate more than once is an important consideration when predicting the descendant population. Pointing (1961) found that under insectary conditions *Rhyacionia buoliana* (Schiff.) males are capable of inseminating more than one female. Stehr (1954) states, with reference to a method of mating *Choristoneura fumiferana* (Clem.) in the laboratory, "After mating, the male may be discarded; only rarely will it mate successfully with a second female." During genetic studies conducted in an insectary on the reproductive capacity of four species of *Choristoneura*, a technique was used in which individual males were mated to several females. The purpose of the study was to gain genetic information and not to measure sexual activity so that maximum mating opportunities for the males were not provided. In the light of Stehr's observation, it was decided to publish these results since they provide valid but limited information concerning the polygamous capabilities of *Choristoneura* males.

Materials and Methods

The males of two species, *C. fumiferana* (Clem.) and *C. pinus* Free. and interspecific hybrids between them and with the western one-year-cycle budworm from Clinton, British Columbia, *Choristoneura* sp., were used in the experiments. The males were mated to various types of hybrid and non-hybrid females.

On the first day that adults of both sexes were available, pairs less than 16 hours old were selected for mating and placed in six-inch cubical cages. The cages were checked every 15 minutes and the time of each mating recorded. After copulation the females were transferred to eight-ounce jars containing foliage suitable for oviposition. On the following days, those males *from which further matings were desired* were supplied with fresh females, and additional pairs of newly emerged adults were set up for mating. The ovipositing females were checked daily and the laid eggs counted. A month later, the egg clusters were then checked and the unhatched eggs counted.

TABLE I

The percentage success of *Choristoneura* males observed in polygamous matings.

Male* genotype	1st matings		2nd matings		3rd matings		4th matings	
	Obs.	% success	Obs.	% success	Obs.	% success	Obs.	% success
B♀ × B♂	49	69	17	65	3	33	1	0
J♀ × J♂	34	79	10	90				
B♀ × J♂	18	67	6	50	2	50		
J♀ × B♂	14	78	3	100	1	100		
B♀ × D♂	3	100	2	0	1	100	1	100
D♀ × B♂	37	87	17	76	5	100		
Total	155	76	55	71	12	69	2	50
Egg sterility	12%		12%		13%		22%	

*Species origin of parents: B — *C. fumiferana*; J — *C. pinus*; and D — *Choristoneura* sp.

Results and Discussion

The success of *Choristoneura* males in polygamous matings is summarized in Table I, where genotype designates the parentage of the males; per cent success is the proportion of mated females that laid fertile eggs and is grouped according to whether it was the first, second, third, or fourth mating by the male; and egg sterility denotes the portion of the eggs laid by fertile females that failed to hatch. The difference between the number of males that mated once and the number that mated two or more times should not be interpreted as a measure of the proportion of males capable of mating any given number of times nor as the maximum mating frequency for individual males, since in most instances the opportunity was limited; often only one or two matings were desired of a particular male. Moreover, never more than one female was provided each day although at least some males could have mated more than once, females being receptive over a ten-hour period (Smith, 1954) and copulation often lasting much less than the average 4½ hours reported by Smith (1953).

Quite clearly, previous matings *per se* do not lower the ability of a male to mate successfully. During the first three days of adult life there is no decrease in sperm viability as indicated by the constancy of egg sterility. The slight decline in mating success, if significant, is undoubtedly the result of ageing, which is expected to reduce the potency of any male regardless of previous sexual activity. Moreover, previous matings certainly do not diminish the willingness to mate since approximately 85 per cent of females caged with non-virgin males were mated compared to 65 per cent of those placed with virgin males. Indeed the more virile males of a field population may well mate with so many females that they prevent the weaker males from contributing to the gene pool of the next generation. There is certainly no physical factor limiting the males to one successful mating; one individual, caged with a female having a blocked copulatory duct, attempted to force in 10 spermatophores during a six-hour period.

Other than the duration of each copulation in relation to the receptive period of the females, longevity probably is the only factor limiting the mating capabilities of these males. An approximate average and maximum life span for each of the types of males studied here was: J—three and five days, BxD—seven and 12 days, and all others—four and seven days, respectively. Stehr (1954) disregarded the age factor in handling the males and this undoubtedly led to the erroneous conclusion that males will rarely mate successfully with a second

female.   Often the males were stored at 42°F. for two or three days before a female was provided and then they were held with the first female for three or four days before a second female was supplied. In view of the short life span of *Choristoneura* males it is not surprising that second matings were rare.

It has been demonstrated here that males in captivity are capable of mating several times. After observing for seven seasons the mating behaviour of *Choristoneura* males, I cannot conceive of a capable male, regardless of its previous sexual activities, remaining passive to a receptive female, whether in captivity or in the wild. In the experiments reported here, 155 males were sufficient to supply mates for 224 females so that it would be incorrect to consider a shortage of males as a "mortality factor" in life-table studies of any member of the genus *Choristoneura*.

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(Received May 3, 1961)

Studies of Predators of the Balsam Woolly Aphid
Adelges piceae (Ratz.) (Homoptera : Adelgidae)
IX. *Pullus impexus* (Muls.) (Coleoptera : Coccinellidae), An Introduced Predator in Eastern Canada[1,2]

By R. C. CLARK[3] AND N. R. BROWN[4]

Pullus impexus (Muls.) is one of many species of predators that have been introduced into Eastern Canada since 1933 as part of a biological control program against the balsam woolly aphid, *Adelges piceae* (Ratz.) Delucchi (1954) has published many details of the systematics, biology, and natural control of this species in Europe where he found it to be associated with all *A. piceae* infestations. According to Pschorn-Walcher and Zwölfer (1960), it is one of a group of predators that are usually associated with lower population densities of *A. piceae* and other related adelgids, than are *Aphidoletes thompsoni* Möhn and *Laricobius erichsonii* Rosen. Because it is common on adelgid infestations in Europe and because it can easily be reared *en masse*, large numbers have been released in North America. The purpose of the present paper is to bring together available information on releases, life-history and natural control, and control value of this species, obtained from studies carried out over the past nine years in New Brunswick.

P. impexus adults, collected in Europe, were released in Canada each year 1951-1960 inclusive, with the exception of 1956 (Table I). Most early releases were made in the vicinity of Fredericton, N.B., where the performance of the predators could most conveniently be studied. The adults were released at the

Locality	No. released	Year
NEW BRUNSWICK		
Area 3, McLeod Hill Road, Fredericton	1471	1952
Area 4, U.N.B. Forest, Fredericton	2610	1952
Area 5, U.N.B. Forest, Fredericton	1072	1951
Area 6, U.N.B. Forest, Fredericton	2500	1951
Area 8, U.N.B. Forest, Fredericton	1085	1952
Area 9, Hanwell Road, Fredericton	2177	1952
Area 10, O'dell Forest, Fredericton	1115	1953
Area 12, Old Springhill Road, Fredericton	2414	1953
Area 13, Old Springhill Road, Fredericton	8134	1953
	22578	
Skiff Lake, York Co.	2494	1954
Oak Bay, Charlotte Co.	2507	1954
Moore's Mills, Charlotte Co.	1883	1954
Salisbury, Westmorland Co.	2109	1954
Petitcodiac, Westmorland Co.	1483	1954
Rexton, Kent Co. (two locations)	2063	1954
Bass River, Kent Co.	3138	1954
	15677	
NOVA SCOTIA		
Riversdale, Colchester Co.	2139	1952
McCallum Settlement, Colchester Co.	120	1955
	2259	
NEWFOUNDLAND		
Robinson's Station	1306.	1952
Flat Bay Brook	1534	1953
Nardinis	2570	1954
Wild Cove, Humber	2000	1954
Wild Cove, Humber	420	1960
45.2 mi. W. Corner Brook	890	1955
John's Beach	464	1957
Frenchman's Cove	519	1958
Frenchman's Cove	3500	1959
South Brook	6000	1959
Corner Brook	726	1960
	19929	
Total released 60,443		

bases of trees on which populations of *A. piceae* were high. Some were also released in cages of the type described by Clark and Brown (1958) to facilitate study of their behaviour.

Yearly surveys for *P. impexus* were made in each release area in New Brunswick beginning in the year following release. These were carried out when the predator was in the late larval instars because it is most readily found at that time. At each survey point the basal six feet of trees with all degrees of aphid infestation were examined carefully for the predator larvae.

For one or two years following release, recoveries of *P. impexus* larvae were made at most of the release points. Dispersal was limited and the maximum recorded spread after two years was only 400 yards. In subsequent years fewer specimens were recovered each year until 1960 when none were found. These

recovery records indicate that the species is apparently unable to survive in New Brunswick.

Life History and Description of Stages

P. impexus is univoltine (Fig. A). Oviposition occurs from September 1 to October 15 and the egg is the usual overwintering stage. Eggs are deposited singly in bark crevices, on the underside of lichens or in other protected places, and are attached to the bark by a colourless adhesive which makes them difficult to dislodge without damage. The eggs (Fig. 1) which are 0.60 mm. long and 0.35 mm. wide, are deep red when viewed through a hand lens, or dark orange when viewed through a microscope. They are oval in outline and are distinctly rounded at each end. The surface is smooth and shiny under low magnification but appears irregularly sculptured into roundish areas under high magnification.

Hatch begins about May 10 and continues until about May 31. Larvae may be found until nearly the end of June but maximum numbers are present from May 25 to June 10. Length of larval life averages three weeks. Larvae (Figs. 2 and 3) when newly hatched are 1 mm. long and when fully grown 5 mm. long. Newly hatched larvae are light orange, changing to darker orange in later instars. All instars are elongate-oval shaped with the anterior end broadly rounded, and the posterior end bluntly wedge-shaped. The dorsum is arched and the venter flat. Segments of the thorax and abdomen are densely covered with a pure white, waxy secretion which is whiter than *A. piceae* 'wool'; it reforms on each instar shortly after ecdysis. Segmentation is distinct and appears as bands of black and white as the larva moves. The integument is sparsely covered with minute setae which are not visible when the white, waxy secretion is present. The fourth-instar larvae spin cocoons of pure-white, silky threads (Fig. 4) usually in bark crevices. The prepupa is usually visible through the cocoon.

P. impexus larvae feed voraciously on all stages of *A. piceae*. Delucchi (1954) observed one second-instar larva devour practically all *A. piceae* stages on 10 cm.^{2} (4 ins.^{2}) of densely infested bark in four days. In discussing the feeding of fourth-instar larvae he further observed that "the destruction of an egg does not require more than ten seconds and one larva destroys whole broods in rapid succession". He found that in some instances aphid infestations, heavy enough to make tree trunks appear whitish over large areas, were completely destroyed by *P. impexus* larvae along with just a few individuals of other predacious species.

The pupal period, which lasts ten days, occurs between June 1 and July 15, with maximum numbers from June 15 to July 1. Pupae (Fig. 5) are 3 mm. long, 2 mm. wide, and dark yellowish-orange with distinct segmentation and smooth integument. They are found within the fourth-instar cocoon.

Adult emergence begins about June 15 and ends about July 31. Mating and oviposition do not begin until September 1, and oviposition is usually completed by October 15. Adults decrease in numbers from mid-September until frost occurs, but some overwinter. They have been recorded in June of the following season, but feeding, mating, or oviposition have not been observed at this time. Delucchi (1954) found that many adults overwinter in Europe and become active when the temperature rises to 50°-60° F. These feed, mate, and oviposit, but the eggs laid are not viable.

Adults (Fig. 6) range in size from 2.5-3.0 mm. long and 1.5-2.0 mm. wide. The general colour of the dorsum is dull orange but the pronotum is slightly darker. The compound eyes are brownish-black and the venter and legs are
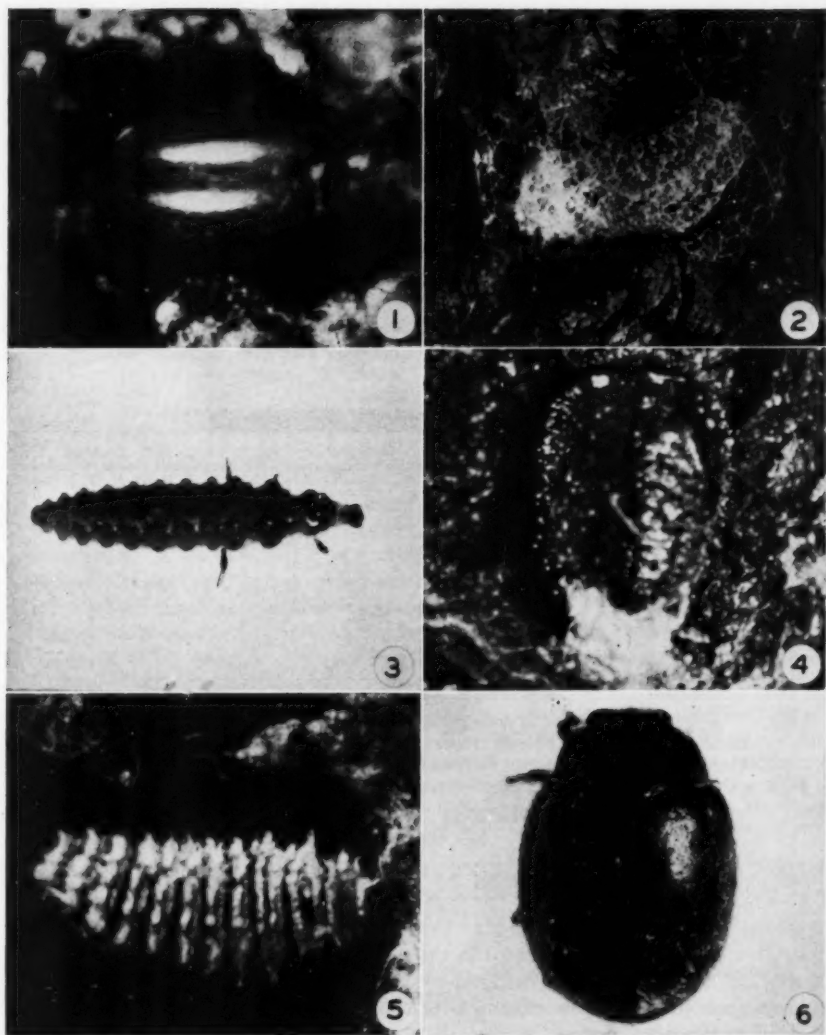
Figs. 1-6. *Pullus impexus*. 1, egg; 2, cocoon; 3, larva, instar IV without wax covering; 4, pupa; 5, larva, instar IV with wax covering; 6, adult.

dark orange.   All surfaces including legs have a short vestiture which does not obscure the general coloration.

During the summer, adults feed on all stages of *A. piceae*, but eggs, nymphs, and adults form the bulk of the food material and only a few 'crawlers' and neosistentes are consumed.   When feeding, the adults completely obscure the adelgid being eaten.   Adult feeding habits are described in detail by Delucchi (1954) and Smith (1958).

When released, *P. impexus* adults quickly became very active, crawling or sometimes flying to the tree trunks.   Most rested on the bark and a few crawled
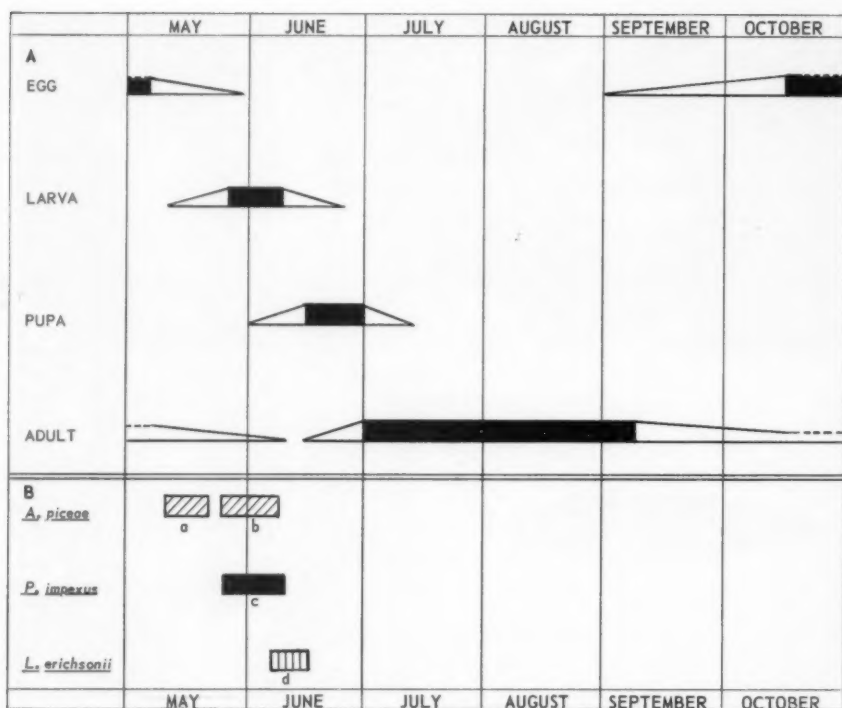
Fig. 7. A. Life cycle of *Pullus impexus* (Muls.) based on data from 1952 to 1955. Solid areas represent normal periods of occurrence; clear areas indicate extreme ranges. B. Development of some stages of *A. piceae*, *P. impexus* and *L. erichsonii* based on data from 1952 to 1955. (a) First *A. piceae* eggs laid by hiemosistentes. (b) Maximum *A. piceae* intermediate stages and adults, hiemosistentes. (c) Maximum *P. impexus* larvae. (d) Maximum *L. erichsonii* larvae.

slowly up the tree trunks, but none were observed more than 1½ feet above the release point after 45 minutes. A few fed soon after release. No mating was observed at this time but this was to be expected as they had emerged but a few days previously. When observed in the field at other times, adults were usually resting either exposed or in sheltered places. The slightest jar of the tree trunk or sometimes just a shadow passing over those in full sunlight would cause them to drop to the ground.

Natural Control

Low winter temperatures appear to be the most important natural control factor in New Brunswick, and *P. impexus* recoveries during the past nine years show a relationship to the low temperatures experienced the preceding winters. Following the winters 6f 1952-53 and 1953-54, when the minimum temperatures were −11° F. and −19° F., *P. impexus* was recovered in moderate numbers in most of the release areas. Following the winter of 1954-55, when the minimum temperature was −27° F., very few recoveries were made. There was very little increase in populations during the summer of 1955, and in the summer of 1956 following a minimum winter temperature of −17° F., very few recoveries were again recorded. The minimum temperature during the winter of 1956-57 was −20° F. and the following spring only one larva was recovered during exam-

ination of all release points. Since that time the only recoveries made have been four adults and 15 larvae in 1958, and one larva in 1959. No recoveries were made in 1960. Delucchi (1954) found that all eggs held at 10° F. hatched, but that only 95 per cent of those held at −13° F. hatched. Lower temperatures were not tested, but it is reasonable to assume that mortality would increase rapidly at temperatures lower than −13° F. and in New Brunswick, where winter temperatures of −15° F. to −20° F. are common and extremes of −20° F. to −30° F. are not unusual, a heavy mortality could be expected. From the relationship between *P. impexus* recoveries and low winter temperatures in New Brunswick, and from the work of Delucchi in Europe, it can be concluded that only eggs laid low on the tree trunk and protected by snow cover might be expected to survive the winter in New Brunswick.

In New Brunswick, there has been no evidence of parasitism or predation of *P. impexus* since it was first introduced.

Control Value

In Europe, Delucchi (1954) found that it was difficult to estimate the value of *P. impexus* as a predator and to determine its relationship to other predators associated with it. His evaluation of the species was not made on an experimental basis but from field observations during the years 1950 to 1952. He found that *P. impexus* was an effective predator capable of destroying the hiemosistens generation of *A. piceae* over a period of three or four weeks when populations were sufficiently high, and on this basis he concluded that it would be advisable to introduce *P. impexus*, without its parasites, to Canada.

In New Brunswick, following the large-scale releases between 1951 and 1954, *P. impexus* failed to establish and increase as anticipated. In several instances caged colonies of 300-400 adults completely destroyed the heavy infestation within the cages (about 800-1,200 sq. in.), but natural predator populations of this size were never achieved. In one or two instances, predation by larvae on the hiemosistens generation the year following release was sufficient to reduce the aestivosistens generation as did *Laricobius erichsonii* (Clark and Brown, 1958). These populations were unable to maintain themselves and subsequent generations of the predator were completely ineffective.

The later larval instars of *P. impexus* are voracious feeders and prefer the eggs of *A. piceae* as food. Like *L. erichsonii* (Clark and Brown, 1958) their time of occurrence is ideally synchronized with the egg stage of the hiemosistens generation of *A. piceae* (Fig. 7B). The one factor that appears to limit the species from becoming numerous, thereby negating the above advantages, is its inability to survive low winter temperatures.

Summary

Following preliminary investigations in Europe, *Pullus impexus* (Muls.) (a predator of *Adelges piceae* (Ratz.)), was introduced in New Brunswick, Nova Scotia, and Newfoundland in the years 1951 to 1960. Studies over the past nine years have indicated that it has failed to establish and increase as anticipated. This is attributed to high winter mortality.

All stages and the life-history and habits are described.

Acknowledgments

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(Received May 23, 1961)

Book Review

Specification for Pesticides: Insecticides, Rodenticides, Molluscicides, Herbicides, Auxiliary Chemicals, Spraying and Dusting Apparatus. Second Edition, 1961; 523 pages, 31 figures, 2 tables. World Health Organization, Palais des Nations, Geneva. Price $10.00 (Clothbound).

The first edition of this manual was published in 1956. By comparison the current edition is considerably enlarged by the inclusion of a range of new pesticides and formulations. An entirely new section on herbicides has been added and the other sections expanded. There have been no changes in the specifications for spraying and dusting apparatus.

The various members of the World Health Organization Expert Committee on Insecticides are to be congratulated for the intensive effort that is reflected by this manual. It is primarily of value to both the manufacturers and users of pesticide products and application equipment. The full WHO purchase specifications are outlined, including laboratory methods for acceptance standards. The authors have had to be realistic in accepting that a specification is almost always a compromise between what industry can make, what the user wants, and what he is prepared to pay for the product. They have also had to bear in mind that sometimes the physical or chemical properties desirable to meet certain requirements will conflict with those criteria governing biological efficacy. This manual reflects a cooperative effort to reconcile these differences between the chemical, engineering, and biological approach at the international level. This is an activity that might well be encouraged and emulated in agriculture.

The specifications are clear and concise. The analytical procedures are better than those in most text books. As yet the specifications for spraying and dusting equipment are restricted to relatively simple compression sprayers, hand sprayers, stirrup-pump-type sprayers and simple hand dusters. It is to be hoped that eventually specifications may be developed for thermal aerosol generating equipment, cold pressure aerosol equipment, and equipment for the application of sprays and granular material from the air.   H. Hurtig

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